The Dissertation Committee for David Allan Raichlen Certifies that this is the approved version of the following dissertation:

The Relationship Between Limb Muscle Mass Distribution and the Mechanics and Energetics of Quadrupedalism in Infant Baboons (*Papio cynocephalus*)

Committee:

Liza Shapiro, Supervisor

John Kappelman

Susan Larson

Deborah Overdorff

Marcus Pandy

The Relationship Between Limb Muscle Mass Distribution and the Mechanics and Energetics of Quadrupedalism in Infant Baboons (*Papio cynocephalus*)

by

David Allan Raichlen, B.S., M.A.

Dissertation

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Doctor of Philosophy

The University of Texas at Austin

August, 2004

Dedication

For Fredric and Judy Raichlen

No words can express how supportive you have been.

Thank you.

Acknowledgements

I would like to thank my supervisor, Liza Shapiro. From the first day I arrived until the end of my graduate studies she has provided me with advice, support, and friendship. Liza has provided me with everything that has been needed to complete this dissertation and through it all, I have learned more than I could have hoped.

I would also like to thank my committee members. In addition to providing excellent feedback on my dissertation, each has had a unique influence on me throughout my career. John Kappelman has shown me many interesting teaching techniques that will certainly be useful in future classes. Susan Larson's work has provided a foundation for the study of primate quadrupedalism, and her research is a major inspiration behind this project. Additionally, her advice on this project, especially in its early stages, was essential in gaining outside funding. Deborah Overdorff has been there whenever advice is needed. Especially in my first couple of years at UT, Deborah helped me become a better writer through her excellent editing skills. She also has been and will be an excellent person to help expand ideas about primate locomotion learned in the lab into more naturalistic research programs. It was Marcus Pandy's biomechanics course that fostered the beginnings of this dissertation project. He is an excellent teacher, and I learned much of what I needed to know to complete this project from him in that class.

I would also like to thank the people and institutions that made my research possible. First, Jody Jensen's generosity has been essential to this project. She freely gave access to her lab and equipment, without which this dissertation would have been impossible. I will always owe her a debt of gratitude for her help. Thanks to Jerry Fineg and Jim Letchworth as well as the animal care staff at the University of Texas Animal Resource Center for their help in caring for our research subjects. Thanks to Dee Carey and Karen Rice for facilitating our access to baboons at the Southwest Foundation for Biomedical Research.

Finally I would like to thank my colleagues in the Department of Anthropology at The University of Texas at Austin. Adam Gordon and Robert Scott were always there for help when needed, breaks when needed, and blowing off steam when needed. I can't thank them enough. Magdalena Muchlinski and Katherine Whitcome gave up their time to help care for our baboons and to help set up our equipment on research days. This project could never have been done without them. Laura Alport, Steig Johnson, Murat Maga and Stacey Tecot have been great friends and commiserators throughout the years and Austin would not have been the same without them. Finally, thanks to all others in Austin who made my years here so much fun.

The Relationship Between Limb Muscle Mass Distribution and the Mechanics and Energetics of Quadrupedalism in Infant Baboons (*Papio cynocephalus*)

Publication No._____

David Allan Raichlen, Ph.D.

The University of Texas at Austin, 2004

Supervisor: Liza Shapiro

Primates have more distally distributed limb mass than many other mammalian quadrupeds because of their adaptations for grasping hands and feet. Although researchers have noted primates' unique limb shape, the effects of this limb mass distribution pattern on quadrupedal mechanics have yet to be examined. Some researchers have predicted that distally distributed limb mass produces relatively low stride frequencies. Others have predicted that distally distributed limb mass leads to increased energetic costs of locomotion because distal mass requires more work to move the limbs during locomotion.

This study uses an ontogenetic sample of infant baboons (*Papio cynocephalus*) to test these predictions. Infants have mass distributed more distally than adults because infant primates must grasp their mothers' hair during their early development. Infants' limb mass migrates proximally as their need to grasp their mothers' hair decreases with

age. To examine the effects of limb mass distribution on the mechanics of quadrupedalism, inertial properties, quadrupedal kinematics, and mechanical work were measured during ontogeny in a sample of infant baboons.

When the infant baboons are young and have limb mass most distally concentrated, they use lower stride frequencies and longer strides compared to older ages, when limb mass is more proximally concentrated. These kinematic changes have important effects on their mechanical energy outputs. The lower stride frequencies used by infant baboons at young ages mitigates the amount of work it takes to move their limbs relative to their body.

In comparison to other mammals, infant baboons have lower stride frequencies and longer strides. They also do less work to move their limbs, but due to longer strides and therefore larger vertical oscillations of their centers of mass, the infant baboons do larger amounts of work moving their whole body center of mass. As a result, the infant baboons do similar amounts of total work compared to other mammals, suggesting a trade-off mechanism that allows total work to be independent of limb shape.

Overall, the results from this study suggest that the adaptations for grasping hands and feet in primates have had profound effects on their kinematics, while likely having little effect on their total energy expenditure.

Table of Contents

List of Tables

List of Figures

CHAPTER 1

Introduction

An underlying assumption in the analysis of evolutionary changes in morphology is that a potential selective advantage of a modification is a reduction in the amount of energy required to perform a particular task. For researchers in physical anthropology, energetic arguments regarding the costs of locomotion have mostly been considered in the study of the evolution of human bipedalism (see Rodman and McHenry, 1980; Pilbeam, 1986; McHenry, 1991; Steudel, 1996; Leonard and Robertson, 1997a,b; Crompton et al., 1998; Kramer, 1999; Leonard and Robertson, 2001; Steudel-Numbers, 2003; Wang et al., 2003). The importance of energetics in the origins of the more generalized form of primate locomotion, quadrupedalism, has received much less attention. Since many regard quadrupedalism to have been an aspect of the locomotion favored by the earliest primates (Gebo, 1997), and since it has been demonstrated that the form of quadrupedal locomotion displayed by primates differs both kinematically and kinetically from that of other non-primate mammals (Kimura et al., 1979; Alexander and Maloiy, 1984; Vilensky, 1987; Vilensky, 1989; Vilensky and Larson, 1989; Demes et al., 1994; Schmitt, 1994; Larson, 1998; Schmitt, 1999; Larson et al. 2000, 2001; Schmitt and Lemelin, 2002), understanding the role energetics plays in primate quadrupedalism should provide new insights into the selection pressures that may have acted during primate origins.

This study examines the interplay among limb morphology, kinematics, and energetics in an ontogenetic longitudinal sample of infant baboons (*Papio cynocephalus*) to discern whether energetics may have played an important role as a selection pressure acting on early primates. Infant primates undergo substantial changes in limb morphology during their development

(Grand, 1977a; Turnquist and Wells, 1994). Since primates in general differ from other mammals in limb morphological parameters, a longitudinal study provides the opportunity to examine how morphological change might impact locomotor kinematics and energetics within individuals, providing a unique window into the evolution of primate quadrupedalism.

MORPHOLOGY: IMPLICATIONS OF GRASPING HANDS AND FEET

Primates are distinguished as a group by their development and reliance on grasping extremities (Jones, 1916; Le Gros Clark, 1934, 1959; Cartmill, 1972, 1974, 1992). Adaptations for grasping hands and feet include the evolution of large and well-differentiated musculature in the distal limb elements to control these extremities (Grand, 1977b; Preuschoft and Gunther, 1994). By contrast, most quadrupedal mammals (especially cursorial quadrupeds) concentrate limb mass proximally (Hildebrand, 1985). Grand (1977b) empirically determined that quadrupedal primates have a greater proportion of body mass located in their forearms, hands, lower legs, and feet than in their upper limb segments (arms and thighs) when compared to cursorial mammals. Finger and toe flexors along with wrist and ankle deviators constitute the majority of this mass (Grand, 1977b). By contrast, the distal limb segment masses of cursorial mammals are comprised primarily of bone (Grand, 1977b).

Grand's (1977) observations were based simply on comparisons of segment masses among different taxa. The other limb inertial properties (center of mass position, and limb mass moment of inertia) of primates have received little attention in the literature (but see Reynolds, 1974; Vilensky, 1979; Wells and Dementhon, 1987; Raichlen, 2004). These inertial properties allow muscle mass distribution to be placed within a biomechanical context (Vilensky, 1979; Preuschoft and Gunther, 1994; Raichlen, 2004). To date, only a single study has compared all limb inertial properties in a primate taxon to those of non-primates (see Raichlen, 2004).

Raichlen's (2004) analysis of primate inertial properties generally confirmed the findings of Grand (1977b), showing primates to have more distal limb centers of mass and large mass moments of inertia compared to other mammals.

The possible impacts of limb mass distribution patterns on locomotion have been examined in a theoretical context (Hildebrand, 1985; Hildebrand and Hurley, 1985; Dellanini et al., 2003), and an experimental context through the addition of weights to the limbs of quadrupeds and bipeds (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel, 1990a,b; Mattes et al., 2000), but have rarely been explicitly tested under more natural conditions (see Taylor et al., 1974).

Studying the morphological and locomotor ontogeny of infant baboons offers a unique opportunity to examine the development of primate inertial properties as well as its effects on locomotion. Grand (1977a) and Turnquist and Wells (1994) have shown that infant primates generally undergo a transition in their limb mass distribution patterns as they age. At young ages, infant primates have very distal muscle mass concentrations, used for strong grasping of their mothers' hair (Turnquist and Well, 1994). As they age, limb mass becomes more proximally concentrated as propulsive musculature becomes important for independent locomotion (Turnquist and Wells, 1994). This study will examine limb inertial properties in a longitudinal ontogenetic sample of infant baboons to document changes in limb mass distribution patterns with age. Any changes in limb mass distributions will be examined within the context of locomotor kinematics and energetics as described below.

KINEMATICS OF PRIMATE QUADRUPEDALISM

Primate quadrupedalism differs from that of most other mammals in several distinctive ways (Kimura et al., 1979; Rollinson and Martin, 1991; Alexander and Maloiy, 1984; Reynolds,

1987; Vilensky and Larson, 1989; Demes et al., 1990; Schmitt; 1998; Schmitt, 1999; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002). It is possible that primates' unique limb mass distribution patterns may play a role in determining their kinematics (Preuschoft and Gunther, 1994; Raichlen, 2004). Before describing this possibility in detail, a brief description of unique aspects of primate quadrupedalism will be given, and current hypotheses for the evolution of these characteristics will be addressed.

Primate quadrupedal kinematics

Primates differ in their footfall sequences during both walking and running gaits compared to most other mammals (see Muybridge, 1887; Hildebrand, 1966, 1967, 1980**;** Rollinson and Martin, 1981; Vilensky and Larson, 1989; Vilensky, 1989; Schmitt et al., 2003; Shapiro and Raichlen, in press). Primates use a diagonal sequence diagonal couplet footfall pattern while walking, where a hindlimb's touchdown is followed by the contralateral forelimb's touchdown, and these limbs are coupled in time (Hildebrand, 1967; see Fig 1.1a). Most other mammals use a lateral sequence diagonal couplet footfall pattern while walking where a hindlimb touchdown is followed by the ipsilateral forelimb touchdown and the contralateral fore- and hindlimb touchdowns are coupled in time (Hildebrand, 1967; see Fig. 1.1b). When running, primates appear to use an amble as opposed to the trot used by most other mammals (Schmitt et al., 2003). In an amble, footfall sequence is similar to walking gaits, and there is no whole body aerial phase (Schmitt et al., 2003). There are, however, separate forelimb and hindlimb aerial phases in an amble (Schmitt et al., 2003; Schmitt, pers. comm.). In a trot, contralateral forelimb and hindlimb touchdowns are highly coupled in time, usually resulting in a whole body aerial phase.

Primates also differ from other mammals in their quadrupedal kinetics (Kimura et al., 1979; Reynolds, 1985; Demes et al., 1994). Primate hindlimbs experience higher peak vertical substrate reaction forces than their forelimbs (Kimura et al., 1979; Reynolds, 1985; Demes et al., 1994). This pattern differs from that of non-primate quadrupeds, whose forelimbs experience higher peak vertical substrate reaction forces than their hindlimbs (Kimura et al., 1979; Reynolds, 1985; Demes et al., 1994).

In addition to footfall sequence and kinetics, primate quadrupeds use different kinematic patterns compared to non-primate quadrupeds (Alexander and Maloiy, 1983; Reynolds, 1987; Vilensky et al., 1988; Demes et al., 1990; Schmitt, 1994; Schmitt, 1998; Larson, 1998; Schmitt, 1999; Larson et al., 2000, 2001). In general, primates use relatively long strides and relatively low stride frequencies during walking and running (Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1990), have relatively larger limb angular excursions compared to most non-primate mammals (Reynolds, 1987; Larson et al., 2000, 2001), have longer stance durations (Schmitt, 1999; Cartmill et al., 2002), and have greater elbow and knee flexion angles during stance phase compared to most non-primate mammals (Schmitt, 1994; Schmitt, 1998; Schmitt, 1999; Schmitt, 2003; Larney and Larson, in press).

Hypotheses for the evolution of primate locomotion

Several authors have suggested that primates' footfall patterns, kinetics, and their unique quadrupedal kinematics are the result of adaptations for safe travel in an arboreal small branch niche (Demes et al., 1990; Larson, 1998; Larson et al., 2000, 2001; Cartmill et al., 2002; Schmitt and Lemelin, 2002; Schmitt, 2003), an environment presumably important in the early evolution of primates (Cartmill, 1972, 1974; Rasmussen, 1990; Sussman, 1991; Hamrick, 1998).

Cartmill et al. (2002) suggested that a diagonal sequence footfall pattern may be adaptive for negotiating unstable branches in a small branch habitat. According to this hypothesis, in diagonal sequence gait, just before a forelimb touches down on an untested support, the hindlimb is securely gripping the branch underneath the body's center of mass and is able to maintain balance if the forelimb touches down on an unstable support (Cartmill et al., 2002). This hypothesis has, however, recently been called into question because diagonal sequence gait is not the only footfall sequence that achieves this type of limb positioning (see Shapiro and Raichlen, in press).

The unique kinetics of primate quadrupedalism have been attributed to the need to reduce forces on a more mobile forelimb that has undergone adaptations for arboreal use (Demes et al., 1994). Shoulder mobility is an essential arboreal adaptation, yet mobility comes at the price of stability (Larson, 1993), so the forelimb may not be able to withstand high forces (Demes et al., 1990).

Finally, primate kinematics may also be related to safe travel in an arboreal small branch niche (Demes et al., 1990; Larson, 1998; Larson et al., 2000, 2001). In this environment, low stride frequencies reduce potentially dangerous branch oscillations (Demes et al., 1990). At a given speed, low stride frequencies are associated with increases in stride length which, in turn, are created by increased limb angular excursions (Demes et al., 1990; Larson et al., 2000, 2001).

Locomotion in an arboreal small branch niche poses other problems for primates. Primates must maintain a crouched posture to keep their centers of mass close to the substrate for better balance (Schmitt, 1999). A crouched posture will increase the stresses on limb bones and joints because of an increase in the moment arm of the substrate reaction force vector (Schmitt, 1999). To solve this problem, Schmitt (1999) suggested that primates use a compliant walking

style. Compliant gaits, marked by greater knee and elbow flexion angles during stance phase, reduce vertical substrate reaction forces by reducing the vertical oscillations of the center of mass (Schmitt, 1999; see also Larney and Larson, in press). The large angular excursions, long strides and low stride frequencies increase stance durations which further reduce vertical substrate reaction forces by increasing the amount of time over which these forces accrue (Schmitt, 1999). Reducing the vertical substrate reaction force by making kinematic adjustments may be a solution to the otherwise large stresses on the limbs of arboreal primate quadrupeds (Schmitt, 1999).

There is some indication that non-primates who occupy a small branch niche have converged on primate quadrupedal characteristics (Schmitt and Lemelin, 2002), further supporting the small branch niche hypothesis. Specifically, Schmitt and Lemelin (2002) found that, like primates, the wooly opossum (*Caluromys philander*) uses diagonal sequence gait, large forelimb protraction angles (probably leading to large forelimb angular excursions; see also Larson et al., 2000, 2001), and experiences higher hindlimb vertical substrate reaction forces compared to their forelimbs.

Additionally, Schmitt (2003) has shown that the walking mechanics of the common marmoset (*Callithrix jacchus*) differ from those of primate quadrupeds, and resemble the walking mechanics of non-primate quadrupeds. The common marmoset has sharp claws and rarely uses fine branch supports, so Schmitt's (2003) results further support the small branch niche hypothesis for the evolution of primate quadrupedal kinematics.

Although these ideas are compatible with more general theories about the importance of a small branch environment during the evolution of primates (see Cartmill, 1972, 1974; Rasmussen, 1990; Sussman, 1991; Hamrick, 1998), they do not convincingly explain why

primates with clawless grasping hands and feet maintain some of these characteristics when not moving within a small branch environment (especially larger bodied primates who no longer make use of this habitat space at any time). It is implied that the primate quadrupedal mechanics described above should be considered symplesiomorphic for primates (see Schmitt and Lemelin, 2002), and therefore would be retained throughout the order. For this explanation to be valid, each kinematic trait must be considered a heritable character. In the absence of evidence for the heritability of kinematic characters, an explanation for primate kinematics that is tied to primate morphology would provide a more complete explanation for the evolution of primate quadrupedalism and the retention of quadrupedal characteristics in primate quadrupeds regardless of substrate use.

Limb mass distribution and primate kinematics

Primates, with few exceptions, have clawless grasping extremities that probably evolved in a small branch setting (Cartmill, 1972, 1974, 1992). Importantly, primates who no longer use the small branch niche maintain these grasping abilities, using their prehensile extremities for a variety of other tasks (e.g. climbing, food manipulation, etc.). As described earlier, grasping hands and feet require relatively distal limb mass distribution patterns (Grand, 1977b; Raichlen, 2004). This study examines the possibility that limb muscle mass distribution may explain some of the unique kinematic features of primate quadrupedalism described above.

Several authors have suggested that distal limb mass concentrations, such as those found in primates, may have important effects on locomotor kinematics (see Preuschoft and Gunther, 1994; Myers and Steudel, 1997). Myers and Steudel (1997) suggested that relatively distal limb mass distributions should increase a limb's natural pendular period of oscillation (NPP). The NPP is the amount of time it takes the limb to swing through one complete oscillation if it

swings as a true pendulum (Myers and Steudel, 1997). Limb motion during swing phase of quadrupedalism is thought to approximate pendular motion (Mochon and McMahon, 1980, 1981; Hildebrand, 1985; Turvey et al., 1988; Holt et al., 1990; Myers and Steudel, 1997; but see Jungers and Stern, 1983; Whitessely et al., 2000). Therefore, increases in the limb's NPP due to increased distal limb mass should lead to relatively longer swing durations (Myers and Steudel, 1997).

Long swing durations may have a cascading effect by increasing stride duration and therefore decreasing stride frequency (the reciprocal of stride duration) at a given velocity (Preuschoft and Gunther, 1994; Myers and Steudel, 1997). Because velocity is the product of stride frequency and stride length, decreased stride frequencies should lead to relatively long strides. Long strides may be brought about by increases in limb angular excursions (Larson et al., 2000; 2001).

The connection between limb mass distribution and temporal kinematics (stride frequency and swing duration) has been supported by experimental alterations in limb mass distributions in both humans and quadrupeds (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel, 1990; Mattes et al., 2000). In these studies, when loads were attached to distal limb elements, individuals had longer swing durations and lower stride frequencies compared to control conditions (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel, 1990; Mattes et al., 2000). In this study, the relationship between limb mass distribution and quadrupedal kinematics will be explored by examining locomotor kinematics in an ontogenetic sample of infant baboons as they undergo changes in limb mass distribution.

ENERGETICS OF QUADRUPEDALISM

Limb mass distribution may also influence energetic costs. The impact of limb mass distribution on energetics is, however, complicated by both its possible effects on kinematics, and the lack of a clear understanding of the determinants of energetic costs in quadrupedal mammals. Below, I will provide a description of our current understanding of mammalian locomotor energy costs, some possible explanations for these costs, and finally, a description of the possible impacts of limb mass distribution patterns on these energetic costs.

Energy expenditure in mammalian quadrupeds

The determinants of energy expenditure in quadrupeds and bipeds have been the subject of much debate (see Heglund et al., 1982; Taylor, 1985; Kram and Taylor, 1990; Steudel, 1990; Minetti et al., 1999). Energetic costs of locomotion are calculated by measuring the rate of oxygen consumed by animals as they walk and run at steady state over a variety of velocities (see Taylor et al., 1982 for a detailed description of this procedure). If the contribution of anaerobic glycolisis is negligible (measured by taking blood samples and examining the amount of lactic acid in a sample), then the amount of energy derived from 1 mL of O_2 is 20.1 Joules (J; see Taylor et al., 1982).

When this procedure was performed on a wide range of quadrupeds and bipeds, Taylor et al. (1982) found that the rate of oxygen consumption ($\dot{V}_{O_2}$) increased linearly with velocity (v) in all taxa tested (with the exception of the kangaroo). The mass specific rate of oxygen consumption ($\frac{\dot{V}_{O_2}}{M}$) at a given speed is described by a linear equation:

$$\frac{\dot{V}_{O_2}}{M} = b + m * v \qquad (1.1)$$

This equation consists of two components which combined, describe an animal's metabolic energy input at a given velocity. The intercept (b) of equation 1.1 is a postural cost and perhaps a start-up cost (Biewener, 2003), and the slope (m) is the cost of transport (the cost required to move 1 kg of body mass 1 m; Biewener, 2003). When the taxon-specific slopes and intercepts were compared across a wide range of body sizes, an inverse relationship with body mass was found for both. Both the cost of transport and the y-intercept decrease with increasing size. Since these results were discovered, the cause of this systematic decrease has been debated (see Heglund et al., 1982; Kram and Taylor, 1990; Minetti et al., 1999). The hope is that, within the explanation for decreases in costs of transport with increasing body size lies the ultimate explanation for what drives energetic costs for a given individual.

Mechanical work and power

An important possible determinant of energetic costs may be the amount of mechanical work done to move the body during locomotion. Work is the measure of energy flow from one body to another (Winter, 1979). Muscles and tendons do work on segments to move them through any distance. The first law of thermodynamics states that in any system, energy is always conserved. Therefore, if energy is consumed, that energy must either do work, or be released in the form of heat (Winter, 1979). The rate at which work is done is called power and may be most directly related to the rate of O_2 consumption. Therefore, the first place to examine why there are systematic differences in energy consumption among animals of different size is to examine the work and power done by the muscles and tendons of the body.

In the early 1980's, Taylor, Fedak, Heglund, and colleagues tried to determine whether systematic differences in the rate of work done by the muscles and tendons to move the body could explain the costs of locomotion in a broad group of taxa. Total mechanical work and

power may be divided into two major components, internal and external work and power, both of which increase with increasing velocity (see Fenn, 1930; Fedak et al., 1982; Heglund et al., 1982; Taylor et al., 1982; Willems et al., 1995).

The work done by muscles and tendons to move body segments relative to the body's center of mass is called mechanical internal work (see Fenn, 1930; Willems et al., 1995). Internal work depends on the inertial properties of the body segments as well as the segment translational and rotational velocities. The work done to lift and accelerate the body center of mass relative to its surroundings is called mechanical external work (Fenn, 1930). Total work is the sum of the two (Heglund et al., 1982). The rate at which work is done is called power.

Mass-specific mechanical internal, external, and total work rates (power) are all basically independent of body size in mammalian quadrupeds, and almost fully dependent on velocity (Fedak et al., 1982; Heglund et al., 1982; Heglund et al., 1982). It was therefore concluded that mechanical work rates, in and of themselves, are an unsatisfactory explanation for energetic costs.

Energy-saving mechanisms that reduce mechanical work

One reason why work rates may not be related to body size is through the use of energy saving mechanisms that reduce the amount of work done to raise and accelerate the center of mass and to move the body segments relative. These mechanisms will be discussed in detail below, but it is important to note that large taxa appear to use energy-saving mechanisms to a greater degree than smaller taxa (Cavagna et al., 1977; Biewener et al., 1981; Heglund et al, 1982)

During walking, bipeds and quadrupeds employ a pendular exchange between potential and kinetic energy (Fig. 1.2a). As an animal touches down and begins stance phase, the center of

mass is slowed down, while it is vaulted over the limb. By reducing center of mass velocity, while raising it off the ground, potential energy is increased, while kinetic energy is decreased. After mid-stance, the center of mass is accelerated forward, while it falls over the stance limb. Some of the potential energy from the raised center of mass is now converted into forward kinetic energy without muscles and tendons doing work on the body.

The amount of energy that is recovered by this pendular mechanism during walking differs between bipeds and quadrupeds (Cavagna et al., 1977). Bipeds can have up to 70% energy recovery whereas quadrupeds generally do not have higher than 50% recovery (see Cavagna et al., 1977). The reason for this discrepancy is that a biped's two hindlimbs may function as inverted pendula fairly easily, whereas the four limbs of a quadruped may only function as perfect inverted pendula if the touchdowns of forelimbs and hindlimbs are tightly coupled in time.

If a touchdown of a forelimb occurs at the same time as that of a hindlimb, then the two pairs of ipsilateral (during a pace) or contralateral (during a trot) fore/hind couples may function in a comparable way to the two hindlimbs of a biped. Mammalian quadrupeds generally do not have perfect forelimb and hindlimb coupling while walking (see Hildebrand, 1966, 1967, 1980). Therefore, the degree to which forelimbs and hindlimbs are coupled may play a role in determining the amount of energy recovered (Reilly and Biknevicius, 2003). Reilly and Biknevicius (2003) call particular attention to the single foot gaits (see Fig. 1.3), where forelimb and hindlimb footfalls are evenly spaced in time. Use of this gait should reduce the pendular recovery of energy because of a complete decoupling of fore- and hindlimb footfalls (Reilly and Biknevicius, 2003).

In addition to being dependent on gait, the amount of energy an individual can recover by the pendular mechanism increases with increasing size (Cavagna et al., 1977; Heglund et al., 1982). Therefore, the fact that external work rates are size independent may be related to the increased recovery of mechanical energy during the walking gaits of large quadrupeds.

During running gaits, the conversion between potential and kinetic energy is less likely to occur (Cavagna et al., 1977). At touchdown, when the center of mass is decelerating, the stance limb flexes, and the low point of the center of mass trajectory occurs at mid-stance (see Fig. 1.2b). Therefore, as kinetic energy decreases, so does potential energy. After mid-stance, as the limb re-extends, both kinetic and potential energy increase at the same time. Since kinetic and potential energy are largely in phase during running gaits, there is little opportunity to convert potential into kinetic energy. Instead of a pendular mechanism, running animals seem to employ an elastic energy saving mechanism.

The elastic energy saving mechanism has often been described by a spring mass model of running locomotion (Fig. 1.2b; see Farley et al., 1993). When the limb compresses after touchdown, tendons, and muscles to a lesser degree, are stretched and they store elastic energy. As the limb re-extends, this energy is recovered and used for propulsion, thereby reducing the amount of work the muscles and tendons must actually do on the body to perform this acceleration.

In addition to reducing external work, elastic storage and recoil may play an important role reducing internal work (Steudel, 1990). When loads are affixed to the distal limb elements of dogs, both internal work and metabolic costs increased over the control condition, but internal work increases at a higher rate (Steudel, 1990). One mechanism that may allow these different rates of increase to occur is the storage and release of elastic strain energy (Steudel, 1990). This

energy saving mechanism would reduce the metabolic costs of moving heavier limbs or large taxa, despite the increase in the mechanical work done.

There is a difference in the amount of elastic energy savings available to large and small mammals (Biewener et al., 1981; Heglund et al., 1982). Small mammals do not appear to save energy by storing mechanical energy in elastic structures (Heglund et al., 1982). In fact, Biewener et al. (1981) have shown that the tendons of small mammals may be too thick to store elastic energy.

Pendular and elastic energy saving mechanisms play an important role in reducing both internal and external work in mammalian quadrupeds. These mechanisms appear to save more energy for large animals compared to small animals. Size related differences in energy saving mechanisms may therefore play an important role in the size independence of mechanical internal, external, and total work rates.

The Force Hypothesis

Because mechanical work does not appear to explain the energetic costs of locomotion in animals that differ in body mass, many researchers began to suspect that the cost of locomotion may be related to the cost of producing isometric muscle force to support body weight (Taylor et al., 1980; Taylor, 1985, 1994; Kram and Taylor, 1990). Muscles consume energy not only when they do work by shortening (positive work) or lengthening (negative work), but also during isometric contractions (Kram and Taylor, 1990).

Kram and Taylor (1990) suggest that small mammals should have higher metabolic costs because they have relatively higher step frequencies compared to larger mammals. These higher step frequencies would require them to produce force with faster and less economical muscle fibers (Kram and Taylor, 1990; Roberts et al., 1998). These types of fibers require higher rates

of cross-bridge cycling and CA^{2+} pumping, that combined, consume a larger amount of ATP per gram of muscle (Taylor et al., 1980; Roberts et al., 1998). Additionally, there is an activation cost associated with each time the muscle fires (Taylor et al., 1980). The more time a muscle fires in a given distance, the higher the costs due to increases in the number of activation costs (Taylor et al., 1980).

To test this hypothesis, Kram and Taylor (1990) suggested that the force needed to support the body must be inversely proportional to the amount of time a foot is in contact with the ground. This contact time is representative of the amount of time that is available for isometric force production to support body weight (Kram and Taylor, 1990; Roberts et al., 1998). One important assumption of this hypothesis is that the cost of swinging the limbs when not in ground contact is negligible (Kram and Taylor, 1990). The cost of locomotion would therefore not be related to mechanical work, in the classic sense, but would be related to the isometric muscle forces acting to support the body (Kram and Taylor, 1990). Since isometric muscles are not doing positive or negative work, mechanical work should not be able to explain metabolic costs.

Kram and Taylor's (1990) elegant study showed that time of contact increases at a given velocity with increases in body size, and that by introducing a constant, termed the cost coefficient, the rate of metabolic energy consumption ($\dot{E}_{metab}$) can be described by the following equation (from Kram and Taylor, 1990):

$$\dot{E}_{metab} = \frac{cW_b}{t_c} \qquad (1.2)$$

where $\dot{E}_{metab}$ is the rate of energy consumption (W/N), W_b is body weight (N), t_c is contact time (seconds), and c is the cost coefficient (J/N). This coefficient is the proportionality of weight

specific energy cost to the rate of force generation, and is consistent among quadrupeds over a wide range of body sizes (Kram and Taylor, 1990).

Although this hypothesis has been generally accepted by some (see Roberts et al., 1998; Griffin et al., 2003), others have been more resistant. Minetti (1999) suggested that metabolic costs must be some combination of mechanical work done and isometric muscle forces. Additionally, Marsh et al. (2004) have shown that the cost of swinging the limbs is not negligible. In fact, it accounts for up to 25% of the total energetic costs (Marsh et al., 2004). The force hypothesis can't truly be estimating metabolic energy demands on the basis of isometric muscle forces during stance phase if the costs of swinging the limbs are as high as Marsh et al. (2004) have found (Heglund, 2004).

Effects of limb mass distribution on energetics

The discussion above leaves open the question of energetic determinants. What does seem clear, however, is that kinematics play a role (the force hypothesis) and mechanical work plays a role. It is possible that mechanical work plays a role only in so far as all animals of different size do the same amount of mass specific work at a given velocity. Any changes in morphology or kinematics that alter the amount of work done should increase energy expenditures.

Limb mass distribution should have its greatest influence on mechanical internal work. The amount of work done to move limb segments relative to the body depends on both the velocity at which these segments move, and their masses and mass moments of inertia (see Fedak et al., 1982; Hildebrand and Hurley, 1985; Steudel, 1990; Dellanini et al., 2003). The larger the mass, and/or the larger the mass moment of inertia, the more work must be done to move the segment at a given velocity (Hildebrand and Hurley, 1985; Dellanini et al., 2003). Therefore, many workers have suggested that limbs with heavy distal segments (such as those

found in primates) should increase energy expenditures due to increases in internal work (Hildebrand, 1985; Hildebrand and Hurley, 1985; Steudel, 1990; Dellanini et al., 2003).

In addition to influencing internal work, distal limb mass concentrations may reduce an animal's ability to store and recover elastic strain energy in distal limb tendons (Preuschoft and Gunther, 1994). There appears to be a tradeoff between distal muscle size and distal tendon length (Alexander et al., 1981). So, theoretically, individuals with relatively distal limb mass distributions should do more internal work, and more external work, due to their reduced ability to store and recover elastic strain energy, compared to individuals with more proximal concentrations of limb mass. Combined, these increases in work should increase an individual's energetic costs of locomotion at a given velocity.

However, in the only explicit test of the effects of limb mass distribution on the energetic costs of locomotion, Taylor et al. (1974) found that three animals with very different limb mass distribution patterns (the cheetah, the gazelle, and the goat) did not differ in their energetic costs at a given velocity. Additionally, primates do not have significantly different energetic costs compared to other mammals of similar size despite their relatively heavy distal limb segments (Taylor et al., 1982; Heglund, 1985; Steudel-Numbers, 2003). These results touched off a debate in the literature over the true impacts of limb mass distribution on energetic costs that remains unresolved (see Hildebrand and Hurley, 1985; Steudel, 1990).

Mechanical work tradeoff

One possibility is that if limb mass distribution alters locomotor kinematics, then these kinematic changes may influence energetic costs. Distal limb mass distributions should cause low stride frequencies (Steudel, 1990; Preuschoft and Gunther, 1994; Myers and Steudel, 1997). By having human subjects alter their stride frequencies at a given velocity, several authors have found that low stride frequencies actually reduce internal work (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995). If this same pattern is found in a more natural setting,

then the relationship between limb mass distribution patterns and stride frequency may explain the surprising results of Taylor et al. (1974).

Alterations in kinematics may also have important impacts on mechanical external work. Low stride frequencies imply long strides. Long strides lead to increases in the vertical displacement of the body center of mass (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995). Increases in vertical center of mass displacement due to increases in stride length actually increase the amount of mechanical external work done on the body (Cavagna et al., 1977; Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995).

When humans alter their stride frequencies at a given velocity, external and internal work have opposite responses. When summed at each altered stride frequency, total work in humans is curvilinear (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995). Humans tend to walk and run at freely chosen stride frequencies near the minimum of the total work curve (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995). Minetti and Saibene (1992) provide further support for this optimization phenomenon using a mathematical model to predict optimum stride frequencies for humans. These authors suggest a tradeoff between internal and external work as stride frequencies and stride lengths are altered (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995). The results from those studies suggest that the tradeoff between internal and external work is actually an optimizing mechanism (Minetti and Saibene, 1992).

In addition to adult humans and the mathematical model, studies of work in human children have also provided support for this optimization phenomenon (Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004). In running, there appears to be a tradeoff mechanism occurring (Schepens et al., 2001). Children run with higher stride frequencies and

shorter strides than adults, and have larger values of internal work and smaller values of external work compared to adults at a given velocity (Schepens et al., 2001; Heglund and Schepens, 2003). Total work in children while running is very similar to adults at a given velocity (Schepens et al., 2001; Heglund and Schepens, 2003). In walking, the higher stride frequencies of children lead to larger amounts of internal work (Schepens et al., 2004). External work, though, is also higher in the children compared to adults, which seems contrary to the tradeoff mechanism (Schepens et al., 2004). Schepens et al. (2004) showed that children recover a much smaller amount of mechanical energy by pendular means compared to adults, which explains their higher external and therefore total work. So, tradeoffs during walking may be complicated by differences in the use of pendular recovery mechanisms, but tradeoffs in running seem to be valid in humans of different size.

The possibility exists that this type of a mechanical work tradeoff mechanism may be employed by quadrupeds as well, and may be linked to limb mass distributions. There may be an optimal combination of stride frequency and stride length at a given speed for an individual quadruped that is at least partially determined by its limb mass distribution pattern, and that minimizes total work.

The presence of a tradeoff mechanism would convincingly explain why total work does not differ among quadrupeds that are not geometrically similar (i.e. in mammals with relatively distal limb mass concentrations). In this study, the effects of limb mass distribution on mechanical internal, external, and total work will be examined in the ontogenetic sample of infant baboons. The existence of a tradeoff mechanism will also be examined. Additionally, the abilities of the infant baboons to recover mechanical energy by pendular and elastic mechanisms will also be measured to determine the whether their abilities change during ontogeny.

PROJECT OBJECTIVES

A longitudinal ontogenetic analysis of infant baboons provides a unique opportunity for exploring the links between limb muscle mass distribution, kinematics, and the energetics of locomotion. First, an analysis of ontogenetic changes in limb mass distribution will be described (Chapter 2). Next, a model is described that predicts how limb mass distribution may impact locomotor kinematics (Chapter 3). The predictions of this model are tested on the infant baboon sample as they age, and their limb mass distributions change (Chapter 4). Next, the effects of changes in both limb mass distribution and kinematics on mechanical work are examined (Chapter 5). Finally, the results from this study are placed within the context of primate and non-primate quadrupedal evolution (Chapter 6). The limitations of this study and future directions are also discussed in Chapter 6.

FIGURES

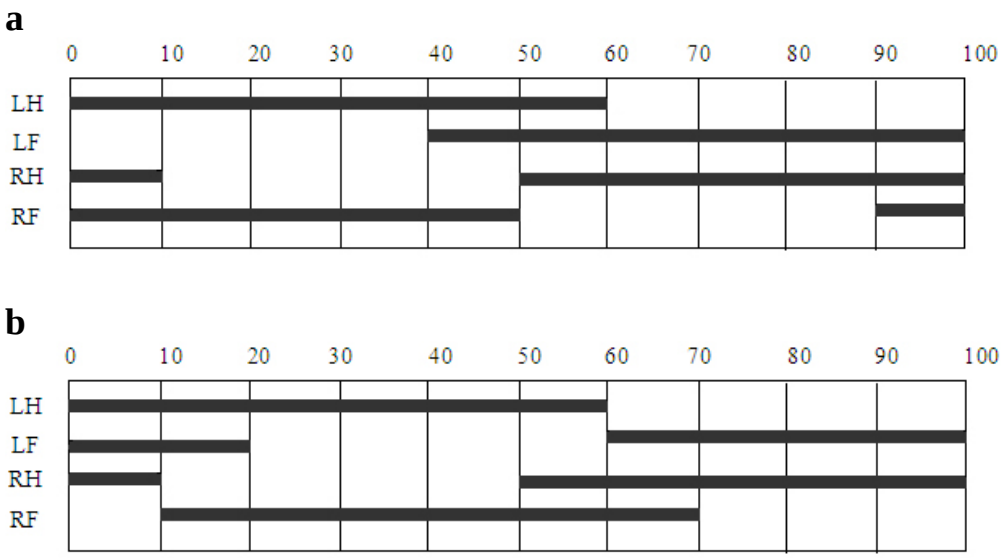


Figure 1.1a,b. Examples of different quadrupedal walking gaits.

Footfall diagrams used as examples of the different walking gaits of mammals. The distance between each vertical line represents 10% of the stride. Ground contact for each limb (left hindlimb, LH; left forelimb, LF; right hindlimb, RH; right forelimb, RF) is represented by black bars. a) Lateral sequence diagonal couplet gait (LSDC) where, after the touchdown of the left hindlimb (0% of the stride), the next forelimb to touchdown is the ipsilateral (left) forelimb (40% of the stride), and the contralateral fore/hind pair is coupled in time; b) Diagonal sequence diagonal couplets (DSDC) where after the touchdown of the left hindlimb (0% of the stride), the next forelimb to touchdown is the opposite side (right) forelimb (10% of the stride), and the contralateral fore/hind pair is coupled in time.

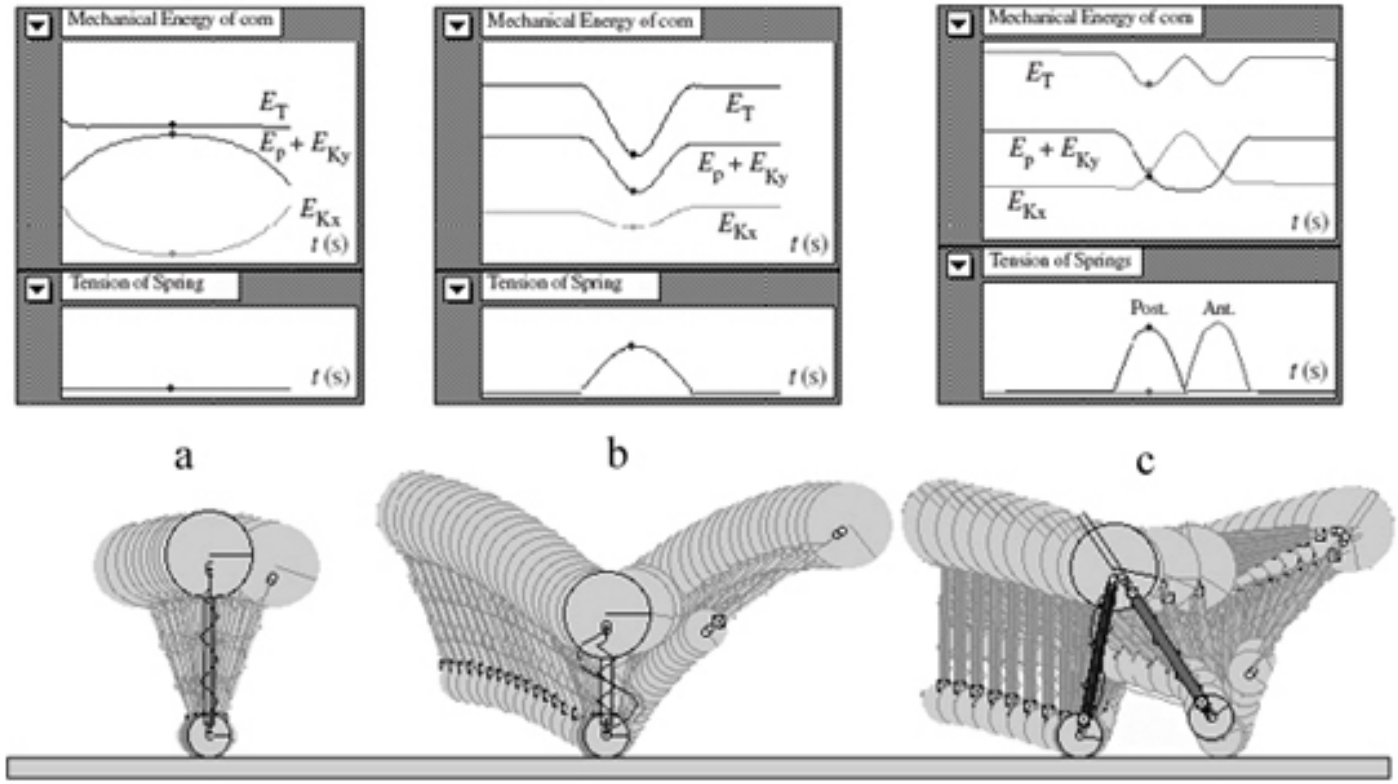


Figure 1.2a-c. Energy saving mechanisms during quadrupedal locomotion.This figure is reproduced from Minetti (1998) with permission from the author. A simulation of walking and running using a pogo stick model with a wheel as the foot is shown in the bottom row of the figure). The top row in the figure shows the energy changes of the center of mass where Ekx is forward kinetic energy, Ep + Eky is the sum of potential and vertical kinetic energy, and ET is the total energy. Below the energy changes is a curve that represents the storage and release of elastic strain energy as a spring on the pogo-stick. a) The pogo stick is modeled as very stiff, and moves as an inverted pendulum, comparable to walking in a biped. Note the complete exchange of potential and kinetic energy resulting in no change in the total energy of the center of mass. b) In running the pogo-stick bounces and kinetic and potential energy are in phase. As the stick compresses, though, elastic energy is stored in the spring and is released as the pogo-stick re-extends. c) In galloping, there is some exchange of potential and kinetic energy and some elastic energy storage and recovery.

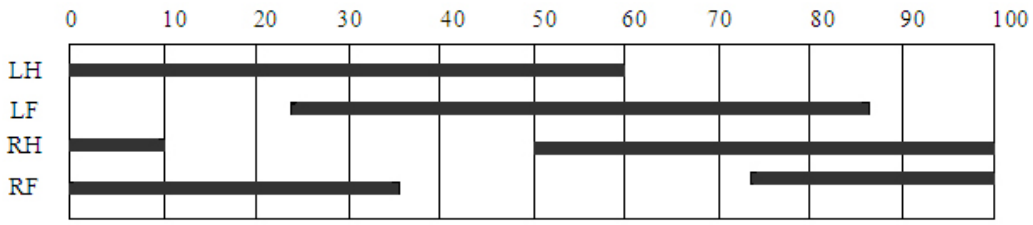


Figure 1.3. Gait diagram of a single-foot walking gait.

As opposed to couplet gaits, in lateral sequence single foot (LSSF) gaits, forelimb and hindlimb touchdowns are evenly spaced in time (i.e. neither the ipsilateral nor the contralateral fore/hind pairs are coupled in time).

CHAPTER 2

Ontogeny of Limb Muscle Mass Distribution in *Papio cynocephalus*

INTRODUCTION

Previous researchers have highlighted important differences in primate limb muscle mass distribution patterns compared to non-primate mammals (Grand, 1977a; Vilensky, 1979; Preuschoft and Gunther, 1994; Raichlen, 2004). Primates in general have mass concentrated relatively distally on their limbs (Grand, 1977a; Preuschoft and Gunther, 1994; Raichlen, 2004). This distal muscle mass corresponds to muscles needed to control grasping abilities in the hands and feet of primates (Grand, 1977a; Preuschoft and Gunther, 1994; Raichlen, 2004); a trait considered to be a hallmark of the order (Cartmill, 1972, 1974, 1992).

Within broad mammalian groups, limb mass distribution patterns differ among taxa depending on differences in limb muscular adaptations. For example, primates that spend a large proportion of time in arboreal settings (climbing, suspensory behaviors, and arboreal quadrupedalism) have relatively more distal limb muscle mass than do more terrestrial primates (Preuschoft and Gunther, 1994; Raichlen, 2004). Among quadrupedal mammals, cursorial mammals tend to have more proximal concentrations of muscle mass compared with non-cursors (Myers and Steudel, 1997), presumably because most cursors have reduced the manipulative abilities of their hands and feet. Finally, differences among dog breeds offer another example of how closely related taxa may differ in limb mass distribution depending on limb functions. Breeds that are considered fighting specialists have greater distal muscle mass compared with

more cursorial dog breeds because they rely on their fore and hind paws for fighting (Pasi and Carrier, 2003).

The possible implications of different limb mass distribution patterns on locomotion have been previously discussed in a theoretical context (Hildebrand and Hurley, 1985; Preuschoft and Gunther, 1994; Myers and Steudel, 1997; Raichlen, 2004) and in an experimental context through the addition of weights to distal limb segments (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel 1990; Mattes et al., 2000). This study will document natural changes in limb mass distribution during infant baboon ontogeny in order to examine the impacts of any changes on the mechanics of locomotion. Additionally, underlying causes for ontogenetic changes in limb mass distributions will be discussed in terms of infant life history patterns.

This study provides the first longitudinal description of the early ontogenetic development of limb inertial properties (mass, center of mass, radius of gyration and mass moment of inertia) in a sample of primate quadrupeds. Limb inertial properties have been described for adult primate taxa (see Reynolds, 1974; Vilensky, 1979; Wells and Dementhon, 1987; Raichlen, 2004), but the ontogeny of limb masses and centers of mass has been described cross-sectionally for only one genus, *Macaca* (Grand, 1977b; Turnquist and Wells, 1994).

In addition to the standard limb inertial properties discussed above, limb natural pendular periods (NPP) are calculated for the infant baboon sample used in this study. The NPP may be an important determinant of kinematics because it approximates swing durations during locomotion (see Myers and Steudel, 1997; Raichlen, 2004). Theoretically, larger limb NPPs should lead to longer swing durations which should in turn affect stride durations (see Myers and Steudel, 1997; Raichlen, 2004). Therefore, the effects of ontogenetic changes in limb inertial

properties are best placed into a locomotor context by examining ontogenetic changes in limb NPPs.

Life history and limb mass distribution

The ontogeny of limb mass distribution in any mammal must be examined within the context of its locomotor development. During ontogeny in *Papio cynocephalus*, most of an infant's travel is done while riding on its mother (Altmann, 1980). Infant *Papio cynocephalus* are able to climb onto the mother's chest under their own power by their second week of life (Altmann, 1980). Ventral riding is the preferred method of travel at the youngest ages, and requires strong manual and pedal grasping abilities to counteract the effects of gravity (as noted for other primate species by Grand, 1977b; Turnquist and Wells, 1994).

During their first few months, infant baboons are, however, able to locomote independently (Altmann, 1980). Indeed, by their second month, infant baboons are able to negotiate obstacles easily, suggesting that coordination is fairly well developed at this early stage of life (Altmann, 1980). By three months of age, infant baboons are generally able to cling to their mothers' backs, and do so for any amount of travel (Altmann, 1980). This form of travel presumably reduces an infant's grasping needs, since gravity helps the infant remain on its mother's back.

The third and fourth months of an infant baboon's life are characterized by increasing independence from its mother (Altmann, 1980). Infant *Papio* are able to play, walk and run in both terrestrial and arboreal settings by this developmental stage (Altmann, 1980). By the fourth month, infant baboons ride on their mothers only for rapid or long journeys, using independent locomotion for all other travel needs (Altmann, 1980). It is important to note that during this time of increasing independence, infant baboons become more responsible for their own welfare

when not in contact with their mothers (Altmann, 1980). It is their responsibility to rapidly return to their mother for group movements or for predator evasion (Altmann, 1980). So, infant baboons' forelimbs and hindlimbs undergo a functional transition during ontogeny from being mainly grasping appendages to having increasingly important locomotor roles.

Presumably, limb mass distribution patterns during development should reflect the changing roles of the forelimbs and hindlimbs in an individual's life history. In previous studies of the ontogeny of limb mass distribution in macaques, it has been shown that limb mass is concentrated most distally at ages when travel is dependent on grasping their mothers' hair (Grand, 1977b; Turnquist and Wells, 1994). It is during the transition from dependent to independent locomotion that limb mass distributions appear to change drastically (Turnquist and Wells, 1994). Limb muscle mass becomes increasingly proximally concentrated during ontogeny in macaques. Independent quadrupedal locomotion requires strong musculature in the proximal segments of both the hindlimbs and forelimbs, and the ontogeny of limb mass distribution in macaques reflects these locomotor needs (Turnquist and Well, 1994).

There is also the possibility that selection acts differently on the forelimbs and hindlimbs during ontogeny (Turnquist and Wells, 1994). It is reasonable to assume that one of the greatest selection pressures acting on infant quadrupeds as they begin independent locomotion is predation (Carrier, 1996). Demes et al. (1994) highlighted the functional differentiation of the forelimbs and hindlimbs during locomotion. They found that in quadrupedal mammals, hindlimbs are net propulsive and forelimbs are net braking.

If selection acts on infant baboons during times of high predation risks, and we assume that hindlimbs predominate propulsion in quadrupeds, then we may conclude that changes in hindlimb propulsive musculature should be heavily selected for as soon as the infant begins to

spend significant amounts of time at a distance from its mother. Since infant baboons still cling to their mothers' backs for long distance and rapid travel well into their first year of life (Altman, 1980), manual grasping requirements may preclude a major reduction in distal forelimb musculature.

Hypotheses

Based on infant baboons' life history patterns, several hypotheses may be made regarding the development of limb inertial properties. Infant baboons are expected to have relatively more distal muscle mass at younger ages, since the infant baboons must rely on grasping abilities more than locomotor propulsive capabilities at early ages, muscle mass is predicted to migrate proximally with increasing age until they approach adult patterns of muscle mass distribution. Additionally, a differentiation of forelimb and hindlimb locomotor roles during ontogeny should be reflected by greater changes in hindlimb compared to forelimb mass distribution patterns (i.e. hindlimb mass should become relatively more proximally concentrated compared to the forelimb as the infant baboons age).

Infant baboons are expected to have relatively more distal limb mass distributions than adult primates over their entire age range, but should be most similar to those of adult primates who have the strongest grasping abilities (i.e. the most arboreal). Additionally, infant baboons should have relatively more distal muscle mass distributions than adult non-primate mammals who have reduced, or non-existent, manual and pedal grasping abilities.

METHODS

Geometric model

This study employs a geometric modeling technique based on one developed by Crompton et al. (1996) and Raichlen (2004) to determine the inertial properties of limb segments (segment mass, position of the segment center of mass, segment mass moment of inertia). This method allowed collection of inertial property data from live subjects. Crompton et al. (1996) developed a geometric model that takes into account the irregularity of limb shape. Their model is based on columns with ellipsoidal cross-sections. Raichlen (2004) made a small improvement on the Crompton et al. (1996) model by allowing the shape of the limb to vary in all directions. The limb of a living animal may then be modeled by taking external measurements along the length of the limb segments (Crompton et al., 1996; Raichlen, 2004).

The model used for this study is based on Crompton et al.'s (1996) and Raichlen's (2004) geometric models with the exception of the fact that in living infant baboons, major and minor axis measurements are exceedingly difficult to obtain due to small body size and time constraints on collecting data from non-anesthetized subjects (subjects were not anesthetized due to safety issues associated with anesthetizing infant animals). Therefore, the body segments of the infant baboons were modeled as cylindrical columns, so that a radius of the column cross section could be calculated from circumference measurements of each limb segment. Equation 1 describes an elliptical cross-section (centered at the origin) where a and b describe the length of the major and minor axis of the ellipse (half the length of the longest and shortest axes of the ellipse; see Fig. 2.1):

$$\frac{x^2}{a^2} + \frac{y^2}{b^2} = 1 \qquad (1)$$

Two curves may then be used to describe the shape of the column (Fig. 2.1). One curve describes how the major axis (*a*) changes with the length of the segment. The other curve describes how the minor axis (*b*) changes with the length of the segment. The length of these curves is equal to the length of the segment.

The shape of the two curves described above were found by taking three measurements of segmental circumference along the length of each limb segment (arm, forearm, hand, thigh, shank, and foot), as well as one measure of the length of the segment (see *Measurement Protocols and Sample*). The circumference was converted into a radius (radius = Circumference/2π) and the radius represented the major and minor axes lengths (a and b in equation 1).

For each segment, the lengths of the major and minor axes were plotted against the measurement position (distance from the proximal end of the segment to the measurement position) and second order polynomials were fit to those data. The inertial properties (mass, center of mass, mass moment of inertia) for these segments were then calculated using equations developed in the appendix.

Calculating inertial properties

Once the inertial properties of all limb segments are calculated, the limb natural pendular period may be calculated assuming the limb acts as a physical pendulum (Myers and Steudel, 1997):

$$NPP = 2\pi\sqrt{\frac{I}{Mg(CM)}} \qquad (2)$$

In equation 2, I is the limb's mass moment of inertia about the proximal joint (the shoulder in the forelimb or the hip in the hindlimb), M is the limb's mass, *g* is acceleration due to

gravitational forces (9.8 m/s^2), and CM is the distance of the center of mass from the proximal joint. The limb NPP is the amount of time it would take the limb to swing through one complete oscillation and may therefore have a large impact on locomotor kinematics.

The calculation of the center of mass of a limb can be found using the following equation (from Tipler, 1976):

$$CM = \frac{\sum_{i=1}^{n} m_i r_i}{\sum_{i=1}^{n} m_i} \quad (3)$$

Where m_i is the mass of the *i*th segment, and r_i is the distance of the center of mass of the *i*th segment from the proximal end of the limb. The denominator is the calculation for the total mass of the limb (M). The mass moment of inertia describes a body's resistance to angular acceleration and can be found using the following equations:

$$I_{cm} = \sum_{i=1}^{n} m_i r_i^2 + I_i \quad (4)$$

$$I_p = I_{cm} + M(CM^2) \quad (5)$$

Where I_{cm} is the whole limb mass moment of inertia about a transverse axis through its CM, I_i is the *i*th segment's mass moment of inertia about a transverse axis through its CM, and I_p is the whole limb mass moment of inertia about a transverse axis through the proximal end of the segment (i.e. the resistance of the limb to angular acceleration during swing phase). Finally, the limb radius of gyration (RG) about the proximal end can be found using the equation (from Myers and Steudel, 1997):

$$RG = \sqrt{\frac{I_p}{M}} \quad (6)$$

This variable is an important measure of overall limb mass distribution as it is the position on a body where a point mass would have an equal mass moment of inertia to the body itself. From equations 3-6, it should be apparent that if limbs carry relatively distal mass, the CM and RG positions will be relatively distal, and I_p will be relatively large.

Measurement Protocols and Sample

Measurements were taken on four live infant baboons (*Papio cynocephalus*) throughout their early development. Each individual was obtained from the Southwest Foundation for Biomedical Research (SFBR) from a population rejected by their mothers and placed in the SFBR nursery. Individuals were housed at the University of Texas Animal Resource Center using methods approved by both the University of Texas Institutional Animal Care and Use Committee (IAUCUC) and the SFBR IAUCUC. At regular intervals throughout ontogeny (twice per month), each infant baboon was placed face down on a soft surface (e.g. towels on a top of a gurney). Segment lengths and circumferences were measured using measuring tape. Segment circumferences were measured at three locations along each body segment (one proximal, one mid-segment, and one distal).

The following segment definitions were used to define the proximal and distal ends of the segments:

a) The upper arm was defined proximally by a point in between the acromion process of the scapula and the greater tubercle of the humerus and was defined distally by the most proximal edge of the radial head.

b) The forearm was defined proximally by the most proximal edge of the radial head and was defined distally by the styloid process of the radius.

c) The hand was defined proximally by the styloid process of the distal radius and was defined distally by the end of the longest digit.

d) The thigh was defined proximally by the greater trochanter and was defined distally by the caudal edge of the lateral condyle of the femur.

e) The leg was defined proximally by the proximal edge of the lateral tibial condyle and was defined distally by the lateral malleolus of the fibula.

f) The foot was defined proximally by the posterior edge of the calcaneus and distally by the tip of the longest digit.

Validity of the Model

Before a geometric model can be used in an analysis of limb shape, its validity must be determined. Two methods were used to determine the validity of the model. First, predicted and measured masses and CMs of limbs and limb segments from adult baboon cadavers were compared. Limbs were removed from the body of one adult baboon cadaver and frozen in a straightened position. Limbs were also removed from the bodies of two other adult baboon cadavers for segmentation. An oscillating saw was used to cut each limb into discrete columns. This procedure eliminated limb flexion as well as extraneous tissue at the proximal ends of the limbs. The total sample for model testing was three whole limbs and six limb segments. The mass of each limb and limb segment was determined experimentally using a scale. The CM position of each limb and limb segment was determined by placing the segment on a tray with a known CM, and balancing the segment/tray unit on a fulcrum (see Meyers & Steudel, 1997). Each limb (n=3), or limb segment (n=6), was also modeled using the geometric column model described above and the measured and modeled values were compared using paired t-tests. Second, body masses of each infant baboon were measured using an electronic scale (nearest 0.1

kg) and then calculated with the geometric model. These values were compared using a paired t-test.

Data analysis

The ontogeny of limb mass distribution was analyzed using three methods. First, each limb inertial property was analyzed using the method of ontogenetic allometry (see Lammers and German, 2002). Limb mass, CM, RG, and mass moment of inertia were regressed against limb length for the entire infant baboon sample. Limb length was calculated as the sum of all limb segments (arm, forearm and hand; thigh, leg and foot). The use of limb length is more appropriate than body mass in this analysis because inertial properties may be more sensitive to changes in limb length than to changes in body mass (see Myers and Steudel, 1997). Reduced major axis regressions were performed to obtain the slope, intercept and estimates of the 95% confidence limits of the slope and intercept for all allometric equations. All infant baboons were analyzed together and individually. The small number of sampled ages for each individual lead to unreasonably large 95% confidence intervals for the within individual analyses that may preclude allometric analysis, so greater weight was placed on the results of combined sample analyses.

Second, limb inertial properties were normalized using dimensional analyses (see also Raichlen, 2004) and compared as the individuals aged. Inertial properties were made dimensionless by dividing each value by a fundamental quantity (or combination of quantities) of the same dimension that is constant in size and biologically relevant (see Hof, 1996). If inertial properties in *Papio* remain geometrically similar during ontogeny, then larger body masses and longer limb lengths should be associated with larger limb inertial property values.

Therefore, the use of body mass and limb length as fundamental quantities removes differences in inertial properties among baboons of different sizes due simply to geometric scaling.

The dimensionless set of inertial properties were constructed after Hof (1996) as follows: limb masses (unit: kg) were divided by body mass, length variables (RG and CM; unit: m) were divided by limb length, NPPs (unit: s) were divided by (limb length/g)$^{1/2}$, (see Hof, 1996 for a complete derivation of the fundamental time quantity) where g is the gravitational acceleration constant (9.8 m/s^2), and mass moments of inertia (unit: kg*m^2) were divided by the product of body mass and the square of limb length. For all inertial properties, Pearson product-moment correlations were calculated for the relationship between dimensionless limb inertial properties and age. A significant correlation indicates a deviation from geometric scaling during ontogeny. The lack of a correlation between a given dimensionless quantity and age indicates geometric scaling.

The dimensionless numbers analysis was done for two reasons. First, the analysis provides a confirmation of the ontogenetic allometry analysis. Second, the use of dimensionless inertial properties may be the only way to compare these values among individuals who differ in body size (see Raichlen, 2004). Therefore, the use of dimensionless inertial properties may be validated for future studies by showing that dimensionless inertial properties show the same trends as the ontogenetic allometric changes in inertial properties in this sample.

Finally, limb segment mass as a percentage of both body mass and limb mass was calculated to compare the infant baboon sample to mass distribution data for other infant primates and adult primates and non-primates. Segment masses as a percentage of limb masses were calculated for a variety of primate and non-primate mammals from the literature. To

compare the infant baboons to these values, 95% confidence limits for the means of dimensionless segment masses were calculated for data taken from the literature.

RESULTS

Model Validity

In the case of both segment mass and CM, the measured and predicted values do not differ significantly for the cadaver sample (Table 2.1). Additionally, measured and predicted masses are highly correlated (r=.998; Fig. 2.2a), as are measured and predicted CMs (r=.996; Fig. 2.2b). Neither regression line differs significantly from the line of identity (y=x; see Figure legend).

Measured and calculated body masses for the infant baboon sample do not differ significantly (Table 2.1). Measured and predicted body masses are highly correlated (r = .974; Fig. 2.2c) and the regression line relating these variables does not differ significantly from the line of identity (Fig. 2.2c). These results support the use of the model for calculating inertial properties and making comparisons of these properties with published values for other taxa.

Ontogenetic allometry

As described in the methods section, the analysis of ontogenetic allometry of limb inertial properties within each individual is complicated by the small number of sampled ages for each individual. These small intra-individual sample sizes create unreasonably large confidence intervals for the slopes of the allometric equations and therefore limit the importance of their analysis. Therefore, for the initial analysis of ontogenetic allometry, all individuals were analyzed together.

Throughout the sampled developmental period for all infants, forelimb and hindlimb lengths grow isometrically (Fig. 2.3; Table 2.2). At a given body mass, hindlimbs are longer than forelimbs. Forelimb mass increases isometrically with forelimb length in the infant baboon sample (Fig. 2.4; Table 2.2). Hindlimb mass increases positively allometrically with hindlimb length (Fig. 2.4; Table 2.2). Over ranges where forelimb and hindlimb lengths overlap, limb masses are similar.

Forelimb and hindlimb CMs increase negatively allometrically with limb length in the infant baboon sample (Fig. 2.5; Table 2.2). The slope of the regression line relating forelimb CM and forelimb length is significantly higher than the slope of the regression line relating hindlimb CM and hindlimb length. Therefore, at a given limb length, forelimb CMs are more distal (larger values) than hindlimb CMs.

Forelimb and hindlimb RGs increase negatively allometrically with limb length in the infant baboon sample (Fig. 2.6; Table 2.2). The slope of the regression line relating forelimb RG and forelimb length is significantly higher than the slope of the regression line relating hindlimb RG and hindlimb length. Therefore, at a given limb length, forelimb RGs are more distal than hindlimb RGs. Finally, forelimb and hindlimb mass moments of inertia increase negatively allometrically with limb length in these infant baboons (Fig. 2.7; Table 2.2). At a given limb length, forelimb mass moments of inertia are slightly larger than hindlimb mass moments of inertia.

In general, as limb length increases, the infant baboons have relatively more proximal CM and RG positions, and relatively lower limb mass moments of inertia. These results are consistent with a proximal migration of limb mass with increases in limb length (and therefore

increases in age). Additionally, the hindlimbs have slightly more proximal concentrations of limb mass compared with the forelimbs at all limb lengths.

An analysis of ontogenetic allometry within each individual infant baboon generally confirms the whole sample analysis described above (Table 2.3). Instances where there is a discrepancy between the individual analysis and the whole sample analysis are shown in bold in Table 2.3. In nine out of the ten instances where an inconsistency occurs, the individual's inertial property increases isometrically, while the whole sample shows either a positive or a negative allometric increase. In these nine cases, the slope of the individual allometric increase agrees with the whole sample analysis, but the 95% confidence limits overlap with isometry. These cases are indicative of small samples leading to large confidence intervals. Only one case (forelimb mass in Infant 1) disagrees in both slope and 95% confidence interval with the whole sample analysis.

Dimensionless inertial properties

The analysis of dimensionless limb inertial properties within each individual infant baboon is also complicated by small sample sizes and the associated difficulties in performing tests of significance. Data for all infant baboons will first be analyzed together, and then the intra-individual analyses will be presented.

For the combined infant baboon sample, dimensionless forelimb and hindlimb lengths are not significantly correlated with age (Fig. 2.8; Table 2.4). At each age, dimensionless hindlimb lengths are larger than dimensionless forelimb lengths.

Dimensionless forelimb mass is not significantly correlated with age in infant *Papio* (Fig. 2.9; Table 2.4). Dimensionless hindlimb mass is significantly positively correlated with age (Fig. 2.9; Table 2.4). Dimensionless hindlimb masses are larger than dimensionless forelimb

masses at a given age. These results are consistent with the results from the ontogenetic analyses showing isometric increases in forelimb mass and positively allometric increases in hindlimb mass with increasing limb lengths.

Dimensionless forelimb and hindlimb CMs are significantly negatively correlated with age (Fig. 2.10; Table 2.4). Dimensionless forelimb CMs are significantly larger than dimensionless hindlimb CMs at a given age. These results are consistent with the negatively allometric increases in both forelimb and hindlimb CM with increasing limb length.

Dimensionless forelimb and hindlimb RGs are significantly negatively correlated with age (Fig. 2.11; Table 2.4). Dimensionless forelimb RGs are larger than dimensionless hindlimb RGs at a given age. These results are consistent with the negatively allometric increase in limb RG position with increasing limb lengths described above.

Dimensionless forelimb and hindlimb mass moments of inertia are significantly negatively correlated with age (Fig. 2.12; Table 2.4). At a given age, dimensionless hindlimb mass moments of inertia are generally slightly larger than dimensionless forelimb mass moments of inertia, and this difference becomes greater at older ages. These results are consistent with the negatively allometric increase in limb mass moment of inertia with increasing limb length described above. The allometric analysis did indicate that at a given limb length, forelimb mass moments of inertia are larger than hindlimb mass moments of inertia. Dimensionless hindlimb mass moments of inertia are larger than those of the forelimb at each age because, at a given *age*, hindlimb lengths are longer than forelimb lengths. These results are not contradictory, but they do highlight the importance of understanding the underlying reasons why a given result is obtained using dimensional analyses.

Finally, dimensionless forelimb are not significantly correlated with age and dimensionless hindlimb NPPs are significantly negatively correlated with age (Fig. 2.13; Table 2.4). Dimensionless hindlimb NPPs are lower than dimensionless forelimb NPPs at a given age.

An examination of the changes in dimensionless limb inertial properties with age within each individual in this sample generally agrees with the whole sample analysis (Table 2.5). In three out of the four infant baboons, when a difference occurs (shown in bold), it is because the individual's sample does not show a significant correlation, but the general trend does not differ (the correlation coefficients have the same signs in the individual analysis compared to the whole sample analysis). Infant 1 shows 4 discrepancies (shown in bold-italics) where the sign of the correlation coefficient differs from those of the whole sample analysis. Again, small sample sizes may be the cause of these discrepancies.

Dimensionless segment masses

Although changes in whole limb inertial properties with age describe changes in whole limb mass distribution, it is important to examine how changes in dimensionless limb segment masses contribute to these overall limb mass distribution changes. For all segments, dimensionless segment masses are calculated at each age in two ways. First, segment masses are calculated as a percentage of body mass. Second, segment masses are calculated as a percentage of limb mass. This second method provides a more direct measure of how limb mass is distributed on a limb regardless of changes in body mass due to changes in either trunk or head mass.

As a percentage of total body mass, arm mass increases significantly with age, hand mass decreases significantly with age, and forearm mass is not significantly correlated with age (Fig. 2.14; Table 2.6). As a percentage of forelimb mass, arm mass increases significantly with age,

hand mass decreases significantly with age, and forearm mass is not significantly correlated with age (Fig. 2.15; Table 2.6). The increase in upper arm mass is likely attributable to increases in propulsive musculature associated with more independent locomotion in older infants.

As a percentage of total body mass, changes in hindlimb segment masses are similar to changes in forelimb segment masses. Dimensionless thigh mass increases significantly with age, dimensionless leg mass does not change significantly with age and dimensionless foot mass decreases significantly with age (Fig. 2.16; Table 2.6). As a percentage of total hindlimb mass, thigh mass increases significantly with age while both leg mass and foot mass decrease significantly with age (Fig. 2.17; Table 2.6). These results highlight a fundamental difference between changes in limb mass distribution in the forelimbs and hindlimbs of infant baboons during ontogeny. The forearm segment does not show a change in dimensionless mass with age indicating perhaps a continuing need for manual prehensility controlled by forearm musculature. The decrease in leg mass relative to hindlimb mass may be due simply to an increase in thigh mass, or may also indicate a decrease in hindlimb prehensility. Either of these interpretations suggests that the hindlimb is becoming the more dominant propulsive limb.

Dimensionless segment lengths

It is important to consider changes in dimensionless segment masses within the context of changes in segment lengths. All segment lengths were divided by the cube root of body mass to make them dimensionless. Dimensionless arm and forearm lengths do not change significantly with age in the infant baboon sample (Fig. 2.18; Table 2.7). Dimensionless hand length decreases significantly with age (Fig. 2.18; Table 2.7). Dimensionless thigh length does not change significantly with age (Fig. 2.19; Table 2.7). Dimensionless leg length increases

significantly with age and dimensionless foot length decreases significantly with age (Fig. 2.19; Table 2.7).

The increase in dimensionless arm mass with increasing age is therefore not due to a change in dimensionless arm length. The decrease in dimensionless hand mass may however be due to a decrease in dimensionless hand length with increasing age. The decrease in dimensionless hand length is consistent with a decrease in manual grasping abilities (See Napier, 1993; Lemelin, 1999).

The increase in dimensionless thigh mass also does not appear to be due to changes in dimensionless thigh length with age. The decrease in dimensionless leg mass occurs despite an increase in dimensionless leg length with age highlighting the reduction in grasping musculature. As with the hand, the decrease in dimensionless foot mass appears to be due to a decrease in dimensionless foot length with age. The decrease in foot length is consistent with a decrease in pedal grasping abilities (see Napier, 1993; Lemelin, 1999).

Comparison with adult *Papio cynocephalus*

In the following section, data from adult *Papio cynocephalus* (from Raichlen, 2004) are compared to the infant baboon sample. The methods used to calculate limb inertial properties in adult *Papio* were similar to those used in the current ontogenetic study. The major difference in methodology was that in adult *Papio*, measurements were taken of the major and minor axes of each limb segment, rather than the circumference measurements used with the infant baboons.

In general, infant baboons have relatively longer limbs than adult *Papio* (Fig. 2.20). Dimensionless forelimb masses are larger in infant baboons compared to adult *Papio* (Fig. 2.21). Dimensionless hindlimb masses are similar to those of adult *Papio* at young ages, and then increase to higher values than adult *Papio* at the oldest ages included in this study (Fig. 2.21).

Dimensionless forelimb and hindlimb CM and RG positions are larger in infant baboons compared to the respective limbs of adult *Papio* at all ages (Figs. 2.22 and 2.23). At all ages, therefore, infant *Papio* has more distal CM and RG positions compared to adults. Dimensionless forelimb and hindlimb mass moments of inertia are larger in the infant baboons than in respective limbs of adult *Papio* at most ages (Fig. 2.24). These results suggest that the infant baboons do in fact have more distal limb mass distribution patterns than adult *Papio*.

Dimensionless forelimb NPPs in the infant baboons do not differ greatly from those of adult *Papio* (Fig. 2.25). Dimensionless hindlimb NPPs in the infant baboons are larger than those of adults at young ages, but do not differ greatly after four months of age (Fig. 2.26). It is somewhat surprising that dimensionless limb NPPs do not appear to be as different in the infant baboons compared to the adults given the more extreme differences in limb CM and RG position and limb mass moments of inertia. These results are, however, consistent with the calculation of limb NPP (see equation 2). Mass moment of inertia is the numerator and limb CM and limb mass are both in the denominator in this equation. Therefore, larger limb mass moments of inertia, coupled with larger limb CMs and masses in the infant baboons may equalize limb NPPs between the infant baboons and the adults. At the ages when dimensionless hindlimb NPPs are greater in the infants compared to adults, infant hindlimb dimensionless masses are similar to adults, so the larger infant baboons' limb mass moments of inertia create larger dimensionless hindlimb NPPs.

Comparison with *Macaca mulatta* during ontogeny

Segment masses as a percentage of limb mass in infant baboons over the sampled developmental period were compared with values from a cross sectional sample of *Macaca mulatta* from one day to one year of age (data from Turnquist and Wells, 1994). Arm masses as

a percentage of forelimb mass in infant baboons are within the range of variation found in rhesus macaques over similar ages (Fig. 2.26). Arm mass as a percentage of forelimb mass increases with age in both samples. Forearm mass as a percentage of forelimb mass is not correlated with age in infant baboons and falls within the range of variation found in rhesus macaques over a similar age range (Fig. 2.27). Finally hand mass as a percentage of forelimb mass appears to drop more steeply in infant baboons compared to infant rhesus macaques, although the baboon values fall within the range of variation of the macaque sample (Fig. 2.28).

Thigh mass as a percentage of hindlimb mass rises at a higher rate in the infant baboon sample compared to the infant macaque sample over similar ages (Fig. 2.29). Both leg and foot masses as a percentage of hindlimb mass fall at a steeper rate in infant baboons compared to infant *Macaca* (Figs. 2.30 & 2.31). The differences between *Papio* and *Macaca* in hindlimb segment mass changes with age may be the result of a greater need for hindlimb propulsive musculature (concentrated around the hip) in the more terrestrial *Papio* coupled with the strong hindfoot grasping needs of the more arboreal *Macaca*.

Comparison with adult primates

Segment masses as a percentage of limb mass in the infant baboons were compared to those of a diverse sample of adult primates from Grand (1977a) and Raichlen (2004; adult *Papio*). It is important to note that the data from Grand (1977a) were obtained from cadavers, rather than the modeling technique used for the infant and adult baboons. The adult primates will be compared to the infant baboons based on the following broad locomotor categories: leaper (*Galago*), strictly arboreal quadrupedalism/suspensory (*Perodicticus*, *Nycticebus*, *Ateles*, *Cebus*, *Aotus*, *Alouatta*), and arboreal/terrestrial quadrupedalism (*Macaca*, *Papio*). These classifications are based on Fleagle (1998).

In general, the leaper and the strictly arboreal primates do not differ significantly in their dimensionless arm masses (Fig. 2.32; Table 2.8). The arboreal/terrestrial quadrupeds have larger dimensionless arm masses than the other primates (Fig. 2.32; Table 2.8). At their youngest ages, dimensionless arm masses are lower in the infant baboons than all other adult primates (Fig. 2.32). As the infants increase in age, their dimensionless arm masses increase, and are more similar to those of most of the other arboreal primates and the leaper. Only the dimensionless arm masses of *Nycticebus*, and the arboreal/terrestrial group (*Macaca* and *Papio*) remain generally larger than the infant baboons at their oldest ages (see Table 2.8).

Dimensionless forearm masses are very similar among the adult primates (Fig. 2.33; Table 2.9). There are, however, some minor differences among the taxa. *Nycticebus* and *Papio* have smaller dimensionless forearm masses compared to the other primates, but again, these differences are slight. Forearm masses relative to forelimb masses are similar in the infant baboons to those of all adult primate taxa (Fig. 2.33). The infant baboons generally have slightly smaller dimensionless forearm masses compared to the leaper and the strictly arboreal taxa, and have slightly higher dimensionless forearm masses compared to *Nycticebus* and *Papio*. These data suggest that forearm mass as a percentage of forelimb mass is quite conservative across primates.

In general, the leaper and the strictly arboreal primates do not differ in their dimensionless hand masses (Fig. 2.34; Table 2.10). *Papio* and *Macaca* have significantly smaller dimensionless hand masses than the other primates (Fig. 2.34; Table 2.10). At their youngest ages, the infant baboons have relatively heavier hands than any of the adult primate taxa (Fig. 2.34). As dimensionless hand mass decreases with age in the infant baboons, their

values become similar to those of the adult primates, with the exceptions of *Macaca* and *Papio* (Fig. 2.34; Table 2.10).

Thigh mass shows more differences among the adult primates than any of the forelimb segment masses (Fig. 2.35; Table 2.11). *Galago*, and *Papio* have the largest dimensionless thigh masses and *Perodicticus*, and *Nycticebus* have the smallest dimensionless thigh mass (Fig. 2.35; Table 2.11). At their youngest ages, the infant baboons' thigh masses relative to hindlimb mass are similar to those of *Perodicticus* and *Nycticebus*, but are lower than those of the other adult primate taxa (Fig. 2.35). As the infant baboons age, their dimensionless thigh masses increase and become more similar to those of the other arboreal taxa. Finally, at their oldest ages, the dimensionless thigh masses are more similar to those of the strictly arboreal quadrupeds (*Aotus, Alouatta* and *Macaca*). The infant baboons do not reach the dimensionless thigh masses of adult *Papio* during this sampled developmental period.

The leaper and the arboreal/terrestrial adults have the smallest dimensionless leg masses of the adult primate taxa (Fig 2.36; Table 2.12). *Nycticebus* and *Perodicticus* have the largest dimensionless leg masses. Dimensionless leg masses in the infant baboons are similar to those of the arboreal taxa at the youngest ages, and as they decrease, become more similar to the arboreal/terrestrial primates and the leaper (Fig 2.36; Table 2.12).

The leaper and the arboreal/terrestrial taxa have the smallest dimensionless foot masses of the adult primates (Fig. 2.37; Table 2.13). *Alouatta* has the largest dimensionless foot mass, and the other primates do not differ significantly (Fig. 2.37; Table 2.13). Dimensionless foot masses in the infant baboons at the youngest ages are higher than those of most other primates with the exceptions of *Alouatta* and *Perodicticus* (Fig. 2.37; Table 2.13). As dimensionless foot mass decreases with age, the infant baboons' dimensionless foot masses become more similar to

those of other primate taxa, but are still higher than the dimensionless foot masses of *Macaca* and *Papio*.

Comparison of infant *Papio* with adult non-primate mammals

In the following discussion comparing the dimensionless segment masses of infant *Papio* with those of non-primate mammals, non-primate mammals are divided into two broad groups following Jenkins (1971): cursorial (*Felis, Canis* and *Equis*) and non-cursorial (*Tupaia, Marmosa, Philander, Didelphis, Caluromys, Monodelphis,* and *Metachirus*). Cursorial mammals are defined by their use of relatively straight limbs during stance phase of quadrupedalism, while non-cursors walk with more flexed elbows and knees during stance phase (Jenkins, 1971). Non-primate segment masses were taken from Grand (1977), Grand (1983), and Sprigings and Leach (1986). This analysis should be treated with caution because 95% confidence intervals could not be calculated for 5 of the non-primate sample because they are represented by a single individual.

With the exception of *Tupaia*, non-cursorial mammals have lower dimensionless arm masses than the cursorial mammals. Interestingly, *Felis* is more similar to the non-cursors than to the more cursorial mammals (Fig. 2.38; Table 2.14). In general, the infant baboons have lower dimensionless arm masses than non-primate mammals (Fig. 2.38; Table 2.14). *Caluromys* and *Didelphis* are most similar to the infant baboon sample.

The cursorial mammals have relatively lower forearm masses than the non-cursors, although *Felis* overlaps with the non-cursorial mammals (Fig. 2.39; Table 2.15). Dimensionless forearm masses in the infant baboons are slightly higher than most of the non-cursorial mammals (Fig. 2.39; Table 2.15). Again, the non-cursorial mammals are most similar to the infant baboons. *Caluromys* has the largest dimensionless forearm mass of all the non-primates, and the

infant baboons have dimensionless forearm masses that are lower than, or equal to, those of *Caluromys*.

Dimensionless hand masses are very similar across all of the non-primate mammals with the exception of the high dimensionless hand mass of the single *Didelphis* individual (Fig. 2.40; Table 2.16). The infant baboons have relatively heavier hands than the non-primate mammals (Fig. 2.40; Table 2.16).

Canis and *Equis* have relatively heavier thighs than those of non-cursors, while *Felis* again overlaps the dimensionless thigh masses of non-cursorial mammals (Fig. 2.41; Table 2.17). The infant baboon sample has relatively lighter thighs than the non-primate mammals (Fig. 2.41; Table 2.17).

The cursorial mammals have much lower dimensionless leg masses with the exception of *Felis* (Fig. 2.42; Table 2.18). At young ages, the infant baboon sample has relatively heavier legs than those of the non-cursorial mammals at young ages (Fig. 2.42). At older ages, the infant baboons converge on the leg masses of the non-cursors and *Felis* (Fig. 2.42; Table 2.18).

Dimensionless foot masses are quite similar among the non-primate quadrupeds (Fig. 2.43; Table 2.19). The infant baboons have relatively heavier feet than the non-primate mammals (2.43; Table 2.19).

DISCUSSION

Biomechanical implications of changes in mass distribution during ontogeny

The ontogenetic allometric analysis and the ontogenetic changes in dimensionless inertial properties highlight a proximal migration of limb mass with age in this sample of infant baboons. The allometric analyses indicate that with increasing limb lengths, the infant baboons have

relatively more proximal CM and RG positions and have relatively lower limb mass moments of inertia. Dimensionless CM, RG and mass moments of inertia all decrease with increasing age. Finally, dimensionless limb NPPs decrease with age in both the forelimbs and hindlimbs. The fact that both types of analysis provide the same results for all inertial property changes confirms the strength of these trends.

There are, however some minor discrepancies when ontogenetic allometry and the dimensionless inertial properties are examined within each individual. These discrepancies may be attributed to the small sample sizes within each individual baboon. Most of the discrepancies are matters of statistical significance and most non-significant trends are consistent with increasingly proximal concentrations of limb mass at older ages.

Previous researchers have noted that limb mass distribution patterns may have large impacts on locomotor mechanics. Distal limb mass concentrations appear to be correlated with relatively long swing durations, low stride frequencies and long strides during walking and running (Preuschoft and Gunther, 1994; Myers and Steudel, 1997). This connection is confirmed by studies showing that distal limb loading in humans and quadrupeds causes increases in swing durations and stride durations (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel 1990; Mattes et al., 2000). Raichlen (2004) has proposed that primates' relatively distal limb mass concentrations may in fact play an important role in their relatively low stride frequencies and long stride lengths (see Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1990). The results from the present study imply that infant *Papio* should use relatively low stride frequencies and long strides at their youngest ages. The hypothesized impact of limb mass distribution on kinematics during ontogeny will be explored in the next chapter.

Forelimb and hindlimb differentiation during ontogeny

The analysis of relative segment mass changes during ontogeny provides some clues about the different selection pressures acting on the forelimbs and hindlimbs. In the forelimb, much of the proximal shift in limb mass is due to the increase in the dimensionless mass of the arm (relative to both body mass and forelimb mass), which occurs with no change in arm length. The dimensionless mass of the forearm remains constant and there is a decrease in the dimensionless mass of the hand which occurs because of a decrease in hand length. As the infant baboons age, the propulsive muscles of the forelimb increase greatly, while the forearm segment continues to retain a significant amount of mass. Forearm muscles are important manual grasping muscles (Grand, 1977a,b) and these results therefore suggest that manual prehensility remains important throughout ontogeny. The decrease in hand mass and length does however suggest a possible decrease in manual grasping importance with age. This interpretation however remains to be tested because the hand may simply reach a limit in length and mass that allows the individuals to maintain grasping abilities to the extent that it needs.

Changes in hindlimb segment mass differ both in magnitude as well as in the contributions of each segment to changes in limb mass distribution. In the hindlimb, there is a large increase in relative thigh mass with age (relative to both body mass and limb mass). This increase is much steeper than that of the relative arm mass and occurs despite no change in dimensionless thigh length. The foot decreases in mass relative to both body and hindlimb mass due to a decrease in foot length and limb mass while the leg decreases in mass relative to limb mass, remaining constant in mass relative to body mass despite increases in dimensionless leg length. The changes in leg and foot mass combined with changes in leg and foot length suggest

that pedal grasping abilities undergo a greater reduction than manual grasping abilities in the infant baboon sample.

These results are consistent with both the beginning of forelimb and hindlimb differentiation in their respective locomotor roles, as well as the possible greater importance placed on hindlimb propulsion at ages when infant baboons stray away from their mothers. Several authors have noted the greater propulsive role of hindlimbs compared to forelimbs in quadrupedal mammals (Kimura 1979; Demes et al, 1994) and this differentiation is reflected in the large increase in dimensionless thigh mass seen in this sample of infant baboons. Because the hindlimb is the propulsive limb in quadrupedal locomotion, its rapid increase in proximal mass may indicate that propulsion is heavily selected at early ages.

Additionally, manual prehension may remain important throughout development, while pedal prehension decreases in its relative importance when an infant reduces the amount of time it grasps its mother's hair during travel. Manual grasping abilities should remain strong through ontogeny as distal muscle mass related to manual grasping is evident in adult *Papio* (see Raichlen, 2004) and is probably most related to foraging (Altman, 1980). The reduction in relative leg mass coupled with little change in relative forelimb masses during ontogeny reflects this possibility.

Comparison of ontogeny in *Papio* and *Macaca*

The comparison of relative segment masses in *Papio* and *Macaca mulatta* during ontogeny highlights the difference in limb muscle mass distribution patterns between more arboreal and more terrestrial quadrupedal primates. *Papio* and *Macaca* have very similar forelimb dimensionless segment mass growth trajectories. Arm and forearm masses relative to forelimb mass do not differ significantly at overlapping ages. The only major difference is that

hand mass relative to forelimb mass may continue to decrease at a higher rate in *Papio*. This difference may be indicative of a decreased need for both manual prehension in a more terrestrial species.

The differences in the hindlimb are more dramatic and likely result from a combination of factors related to the different needs of arboreal and terrestrial quadrupeds. The greater decrease in the relative masses of the leg and foot in *Papio* is most likely related to a decrease in pedal prehensile needs in a more terrestrial quadruped. In macaques, ontogeny is dominated by a large percentage of time spent on arboreal substrates (Wells and Turnquist, 2001), presumably precluding a great reduction in either manual and pedal prehensile capabilities.

These results suggest a fundamental difference in the selection pressures acting during ontogeny in a mostly terrestrial versus a more arboreal primate quadruped. Selection in a terrestrial environment certainly favors the acceleration abilities of infants as they begin to explore the world at a distance from their mothers. As the infant baboons become more independent, it is their responsibility to contact their mothers for group travel or when predation risk is high (Altmann, 1980). Therefore, selection should favor accelerative abilities in infants as soon as they begin to venture away from their mothers.

Comparison with adult primates

At their youngest ages, infant *Papio* have relatively heavier hands and feet, and relatively lighter arms and thighs compared to other adult primates. As they age, and limb mass migrates proximally, the infant baboons' dimensionless segment masses resemble those of strictly arboreal primates, and finally approach the dimensionless segment masses of arboreal/terrestrial quadrupeds. It is interesting to note that the dimensionless forearm masses are similar across a broad range of primate taxa, including the infant *Papio* sample. These results suggest that

forearm mass is quite conservative, and perhaps indicative of the manual prehensile needs of all primates.

The greatest changes in hindlimb segment masses in the infant baboon sample compared to adult primates occur in the leg and foot. Dimensionless leg mass resembles the patterns seen in strictly arboreal primates at early ages. As the infant baboons age, they begin to resemble the relatively light leg masses of adult arboreal/terrestrial quadrupeds. Changes in dimensionless foot mass with age provide the most extreme difference between the infant sample and the adult primates. At very young ages, dimensionless foot masses are higher than all other adult primates, highlighting the importance of intrinsic foot musculature and foot length for early infant grasping abilities. The dimensionless foot masses drop steeply to resemble those of adult catarrhines at older ages.

These results provide a unique view of how limb mass distributions in adult *Papio* result from ontogeny. Selection for reduced grasping musculature coupled with selection for increased locomotor propulsive capabilities has created an ontogeny of limb mass distribution that passes through the limb shapes of other primates with differing substrate preferences. These results strongly suggest the need to collect similar types of comparative data from ontogenetic sequences of more arboreal primates. This type of comparative study would help tease out the timing and relative importance of different selection pressures on primates who have differing locomotor behaviors.

Comparison with adult non-primate quadrupeds

The infant baboons clearly have more distal mass distribution patterns in both their fore and hindlimbs compared to the adult non-primate quadrupeds. The infant baboons do, however, resemble non-cursors and adult domestic cats more than cursorial mammals in their limb mass

distribution patterns. Among the didelphids, *Marmosa, Philander, Didelphis,* and *Caluromys* are considered mostly arboreal quadrupeds (Grand, 1983) and therefore may retain a larger amount of distal musculature than more terrestrial quadrupeds. These taxa have limb mass distribution patterns that more closely resemble those of infant *Papio* than the other mammals included in this analysis. *Felis* uses its paws in prey capture (Taylor et al., 1974) and likely retains some distal musculature for this type of manipulation.

CONCLUSIONS

The hypothesis that infant *Papio* will have a proximal shift in the mass distributions of both the forelimb and hindlimb is strongly supported by the results of this study. Comparisons between the infant baboon sample and adult *Papio* indicate that by 9 months of age, the infant baboons have not yet reached an adult limb mass distribution pattern. The trends for all inertial properties are, however, leading the infant baboons to adult patterns. Even though infant baboons are locomoting independently very early in life, their locomotor musculature is still developing into their late infancy.

The results from this study highlight the early importance of selection acting on hindlimb propulsive capabilities. Manual prehension appears to remain highly important throughout development and therefore, forelimb mass remains relatively more distally concentrated than hindlimb mass. It is possible that it is this early differentiation in forelimb and hindlimb locomotor roles that leads to adult limb mass distribution patterns. Additionally, this study suggests that infant baboon kinematics may shift during ontogeny due to the correlation between temporal and spatial locomotor characteristics and limb mass distribution. It is this possibility that will be tested in the following 2 chapters.

TABLES

Table 2.1 Descriptive statistics for the percent difference data.

property	mean measured	mean predicted	mean % difference	max % difference	min % difference	Paired t-test sig.
Segment mass	996.64	952.22	4.80	14.60	-0.23	.226
CM	11.98	12.30	-2.69	-9.19	0.00	.367
Body mass	1.69	1.71	.53	-23.20	-.03	.294

Note:. Segment mass and CM are from baboon cadaver sample. Body mass is from the infant baboon sample.

Table 2.2 Ontogenetic allometry in infant *Papio* (n=42)

Variable	Isometric Slope	slope	95% CI slope	intercept	95% CI intercept	r^2
Forelimb Length	0.33	0.319	0.029	0.374	0.095	0.926
Hindlimb Length	0.33	0.363	0.037	0.289	0.111	0.910
Forelimb Mass	3.0	3.217	0.228	-2.410	0.353	0.937
Hindlimb Mass	3.0	3.606	0.305	-3.010	0.548	0.926
Forelimb CM	1.0	0.439	0.041	0.674	1.015	0.921
Hindlimb CM	1.0	0.311	0.028	2.852	0.801	0.875
Forelimb RG	1.0	0.517	0.050	0.695	1.215	0.927
Hindlimb RG	1.0	0.364	0.038	3.671	1.133	0.891
Forelimb Inertia	5.0	4.596	0.282	-2.086	0.487	0.949
Hindlimb Inertia	5.0	4.467	0.251	-1.999	0.521	0.958

Note: Length is regressed on body mass, all other forelimb and hindlimb variables are regressed on either forelimb or hindlimb length respectively. 95% CI is the 95% confidence limit of the slope and intercept.

Table 2.3. Intra-individual ontogenetic allometry

Variable (subject)	slope	95% CI slope	intercept	95% CI intercept	r^2	n
Fore Length (1)	0.328	0.055	0.348	0.175	0.973	8
Hind Length (1)	0.398	0.051	0.166	0.163	0.984	8
Fore Mass (1)	**3.404**	**0.267**	**-2.654**	**0.372**	**0.994**	**8**
Hind Mass (1)	3.528	0.31	-2.835	0.444	0.992	8
Fore CM (1)	0.495	0.099	-0.705	2.487	0.962	8
Hind CM (1)	0.309	0.046	2.703	1.287	0.978	8
Fore RG (1)	0.375	0.062	4.236	1.539	0.974	8
Hind RG (1)	0.163	0.144	8.408	3.969	0.562	8
Fore Inertia (1)	**4.866**	**0.223**	**-2.427**	**0.311**	**0.998**	**8**
Hind Inertia (1)	**4.719**	**0.788**	**-2.294**	**1.129**	**0.973**	**8**
Fore Length (2)	0.269	0.11	0.536	0.242	0.882	13
Hind Length (2)	0.332	0.086	0.399	0.28	0.895	13
Fore Mass (2)	2.973	0.519	-2.095	0.734	0.949	13
Hind Mass (2)	**3.276**	**0.572**	**-2.547**	**0.846**	**0.949**	**13**
Fore CM (2)	0.368	0.079	2.611	2.056	0.925	13
Hind CM (2)	0.263	0.121	4.324	3.682	0.73	13
Fore RG (2)	0.351	0.131	4.489	3.401	0.897	13
Hind RG (2)	0.221	0.18	7.036	5.494	0.679	13
Fore Inertia (2)	**4.294**	**0.808**	**-1.695**	**1.142**	**0.941**	**13**
Hind Inertia (2)	4.236	0.486	-1.694	0.72	0.977	13
Fore Length (3)	0.337	0.056	0.307	0.18	0.955	13
Hind Length (3)	0.321	0.074	0.423	0.241	0.915	13
Fore Mass (3)	2.814	0.436	-1.814	0.613	0.96	13
Hind Mass (3)	**3.665**	**0.768**	**-3.09**	**1.13**	**0.928**	**13**
Fore CM (3)	0.428	0.114	0.88	2.962	0.889	13
Hind CM (3)	0.275	0.056	3.936	1.665	0.933	13
Fore RG (3)	0.436	0.135	2.083	3.488	0.857	13
Hind RG (3)	0.207	0.088	7.291	2.65	0.757	13
Fore Inertia (3)	**4.418**	**0.707**	**-1.829**	**0.997**	**0.957**	**13**
Hind Inertia (3)	**4.562**	**0.477**	**-2.154**	**0.702**	**0.981**	**13**
Fore Length (4)	0.3	0.085	0.436	0.272	0.926	8
Hind Length (4)	0.326	0.1	0.409	0.323	0.913	8
Fore Mass (4)	3.028	0.534	-2.913	0.747	0.978	8
Hind Mass (4)	4.706	1.588	-3.718	1.396	0.948	8
Fore CM (4)	0.395	0.066	1.84	1.679	0.973	8
Hind CM (4)	0.27	0.134	4.131	3.888	0.802	8
Fore RG (4)	0.361	0.218	4.898	5.539	0.731	8
Hind RG (4)	0.109	0.152	10.828	4.416	0.338	8
Fore Inertia (4)	**4.789**	**0.994**	**-2.337**	**1.39**	**0.959**	**8**
Hind Inertia (4)	**4.675**	**0.393**	**-2.296**	**0.573**	**0.993**	**8**

Note: Bold faced values do not agree with the combined sample analysis

Table 2.4 Dimensionless inertial property changes with age in infant *Papio* (n=42)

Variable	slope	95% CI slope	intercept	95% CI intercept	r^2	P value
Forelimb Length	-0.006	0.010	2.148	0.050	0.037	0.220
Hindlimb Length	0.006	0.013	2.394	0.069	0.019	0.388
Forelimb Mass	0.000	0.001	0.074	0.005	0.001	0.816
Hindlimb Mass	0.005	0.001	0.087	0.008	0.489	<.0001
Forelimb CM	-0.002	0.002	0.476	0.010	0.115	0.028
Hindlimb CM	-0.007	0.002	0.443	0.010	0.598	<.0001
Forelimb RG	-0.003	0.002	0.556	0.013	0.111	0.031
Hindlimb RG	-0.009	0.002	0.532	0.012	0.606	<.0001
Forelimb Inertia	-0.001	0.0004	0.024	0.002	0.229	0.001
Hindlimb Inertia	-0.0004	0.0004	0.025	0.002	0.104	0.038
Forelimb NPP	-0.010	0.012	5.060	0.063	0.066	0.101
Hindlimb NPP	-0.042	0.014	5.022	0.073	0.486	<.0001

Table 2.5. Intra-individual changes in dimensionless inertial properties with age.

Variable (subject)	r	P value	n
Fore Length (1)	0.15	0.73	8
Hind Length (1)	***0.73***	***0.04***	***8***
Fore Mass (1)	***0.79***	***0.02***	***8***
Hind Mass (1)	0.93	< 0.0001	8
Fore CM (1)	***0.34***	***0.41***	***8***
Hind CM (1)	-0.80	0.02	8
Fore RG (1)	-0.96	< 0.0001	8
Hind RG (1)	-0.94	< 0.0001	8
Fore Inertia (1)	**-0.45**	**0.26**	**8**
Hind Inertia (1)	***0.34***	***0.42***	***8***
Fore NPP (1)	0.14	0.74	***8***
Hind NPP (1)	-0.88	0.004	***8***
Fore Length (2)	-0.28	0.40	13
Hind Length (2)	-0.12	0.71	13
Fore Mass (2)	-0.45	0.14	13
Hind Mass (2)	**0.34**	**0.27**	13
Fore CM (2)	-0.59	0.04	13
Hind CM (2)	-0.67	0.02	13
Fore RG (2)	-0.32	0.31	13
Hind RG (2)	-0.61	0.04	13
Fore Inertia (2)	-0.56	0.00	13
Hind Inertia (2)	-0.40	0.02	13
Fore NPP (2)	-0.20	0.50	13
Hind NPP (2)	**-0.46**	**0.12**	**13**
Fore Length (3)	-0.07	0.84	13
Hind Length (3)	-0.14	0.66	13
Fore Mass (3)	-0.27	0.39	13
Hind Mass (3)	0.79	0.002	13
Fore CM (3)	**-0.14**	**0.65**	**13**
Hind CM (3)	-0.89	0.0001	13
Fore RG (3)	**-0.16**	**0.61**	**13**
Hind RG (3)	-0.85	0.0005	13
Fore Inertia (3)	**-0.17**	**0.16**	**13**
Hind Inertia (3)	-0.47	0.009	13
Fore NPP (3)	-0.33	0.28	13
Hind NPP (3)	-0.89	<.0001	13
Fore Length (4)	0.22	0.59	8
Hind Length (4)	0.05	0.91	8
Fore Mass (4)	0.44	0.27	8
Hind Mass (4)	0.97	< 0.0001	8
Fore CM (4)	-0.79	0.02	8
Hind CM (4)	-0.79	0.02	8

Fore RG (4)	**-0.70**	**0.05**	**8**
Hind RG (4)	-0.97	< 0.0001	8
Fore Inertia (4)	**-0.27**	**0.52**	**8**
Hind Inertia (4)	**-0.37**	**0.36**	**8**
Fore NPP (4)	**-0.93**	**0.0007**	**8**
Hind NPP (4)	-0.91	0.002	**8**

Note: Bold faced values do not agree with the combined sample analysis in significance but do agree in the sign of the correlation coefficient. Italics values do not agree with the combined sample in the sign of the correlation coefficients.

Table 2.6 Segment mass changes in the sample of infant *Papio* (n=42)

Variable	r	p
Arm as a percentage of BM	0.31	0.03
FA as a percentage of BM	0.01	0.93
Hand as a percentage of BM	-0.66	<.0001
Thigh as a percentage of BM	0.80	<.0001
Leg as a percentage of BM	0.27	0.06
Foot as a percentage of BM	-0.67	<.0001
Arm as a percentage of FM	0.59	<.0001
FA as a percentage of FM	0.15	0.30
Hand as a percentage of FM	-0.75	<.0001
Thigh as a percentage of HM	0.69	<.0001
Leg as a percentage of HM	-0.39	0.005
Foot as a percentage of HM	-0.80	<.0001

Table 2.7. Dimensionless segment length changes in the infant *Papio* sample (n=42)

Variable	r	p
Arm	0.02	0.87
Forearm	-0.21	0.12
Hand	-0.50	<.0001
Thigh	0.20	0.14
Leg	0.33	0.01
Foot	-0.40	0.002

Note: Length variables were made dimensionless by dividing them by the cube root of body mass.

Table 2.8. Comparison of infant arm masses as a percentage of forelimb mass to adult primates

Age months	Arm Mass	*Galago*	*Perodicticus*	*Nycticebus*	*Ateles*	*Cebus*	*Aotus*	*Alouatta*	*Macaca*	*Papio*
	Mean	43.06	41.85	47.98	44.03	44.59	45.05	41.01	50.64	57.43
	95% CI	40.93-45.19	39.29-44.41	44.51-51.44	39.91-48.15	42.98-46.2	43.53-46.58	39.22-42.79	48.5-52.78	55.82-59.05
0.73	35.58	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.00	33.96	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.43	33.94	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.47	37.13	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.83	39.29	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
1.97	37.99	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.07	38.20	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.10	42.90	*Equal*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	**Higher**	*Lower*	*Lower*
2.30	42.04	*Equal*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
2.33	40.18	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
2.53	38.02	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.57	39.04	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.80	38.87	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.93	38.98	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.97	40.56	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
3.00	43.87	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
3.23	43.31	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Lower*	**Higher**	*Lower*	*Lower*
3.27	40.67	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
3.47	40.95	*Equal*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
3.50	36.46	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.57	40.53	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
3.60	44.48	*Equal*	Higher	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
3.73	36.43	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.93	40.21	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
4.20	40.24	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
4.40	40.59	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
4.50	40.19	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
4.53	44.40	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
4.67	38.81	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.03	43.93	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
5.07	50.29	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Lower*
5.50	44.10	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
5.53	47.03	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	*Lower*	*Lower*
5.53	47.05	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	*Lower*	*Lower*
5.77	40.91	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
5.80	46.04	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
6.03	39.39	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
6.13	42.29	*Equal*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
6.17	42.54	*Equal*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
6.23	39.02	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.50	44.82	*Equal*	**Higher**	*Equal*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
6.70	51.18	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Lower*
6.97	42.65	*Equal*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
7.17	42.19	*Equal*	*Equal*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
7.37	45.95	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
7.40	44.66	*Equal*	**Higher**	*Equal*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
7.43	44.23	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
8.10	44.78	*Equal*	**Higher**	*Equal*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
8.13	38.83	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
9.00	43.94	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	*Lower*
9.03	43.22	*Equal*	*Equal*	*Lower*	*Equal*	*Equal*	*Lower*	**Higher**	*Lower*	*Lower*

Notes for Table 2.8: Mean segment mass as a percentage of limb mass for adult primates are presented below the name of each taxon along with the 95% confidence limits of the mean. For each infant baboon at each age, **Higher** indicates that the infant value is higher than the upper 95% confidence limit for the mean adult primate value, *Lower* indicates that the infant value is lower than the lower 95% confidence limit for the adult value, and *Equal* indicates that the infant values falls within the 95% confidence limits of the adult value. These conventions will be used for Tables 2.9 – 2. 18.

Table 2.9. Comparison of forearm masses as a percentage of forelimb mass to adult primates.

		Galago	*Perodicticus*	*Nycticebus*	*Ateles*	*Cebus*	*Aotus*	*Alouatta*	*Macaca*	*Papio*
	Mean	41.98942	40.71183	35.4438	38.97465	39.98833	37.44266	38.29397	38.52553	35.04382
	95% CI	40.25-43.73	38.13-43.29	33.45-37.44	38.28-39.67	38.93-41.05	36.49-38.4	36.8-39.79	37.16-39.9	33.79-36.3
Age months	FA Mass									
0.73	37.35798	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
1.00	39.72461	*Lower*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**
1.43	38.01558	*Lower*	*Lower*	Higher	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
1.47	35.21278	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
1.83	36.15491	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
1.97	37.02539	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Lower*	**Higher**
2.07	35.6598	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
2.10	33.63483	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.30	33.44105	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.33	37.37738	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
2.53	33.91983	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
2.57	35.71654	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
2.80	37.34636	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
2.93	38.09334	*Lower*	*Lower*	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
2.97	39.3964	*Lower*	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**	*Equal*	*Equal*	Higher
3.00	33.59963	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.23	35.74914	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
3.27	36.43999	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**
3.47	40.92345	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**
3.50	40.73356	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**
3.57	38.67673	*Lower*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	*Equal*	*Equal*	**Higher**
3.60	37.34041	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
3.73	39.42074	*Lower*	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**
3.93	37.93726	*Lower*	*Lower*	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
4.20	37.37756	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
4.40	37.45988	*Lower*	*Lower*	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
4.50	37.30505	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
4.53	38.42772	*Lower*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	*Equal*	*Equal*	**Higher**
4.67	38.66398	*Lower*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	*Equal*	*Equal*	**Higher**
5.03	35.97832	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
5.07	34.77497	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
5.50	36.62508	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	**Higher**
5.53	35.36848	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
5.53	33.46848	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.77	39.31496	*Lower*	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**
5.80	36.32805	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**
6.03	39.12537	*Lower*	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**
6.13	34.16264	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
6.17	39.76977	*Lower*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	*Equal*	*Equal*	**Higher**
6.23	40.69319	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**
6.50	35.94736	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
6.70	33.6946	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.97	37.46975	*Lower*	*Lower*	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
7.17	38.80274	*Lower*	*Equal*	Higher	*Equal*	*Lower*	**Higher**	*Equal*	*Equal*	**Higher**
7.37	35.62865	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
7.40	36.83275	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Lower*	**Higher**
7.43	36.27948	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
8.10	37.86782	*Lower*	*Lower*	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**
8.13	42.74734	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.00	37.08521	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Equal*	*Equal*	*Lower*	**Higher**
9.03	38.3625	*Lower*	*Equal*	**Higher**	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**

Table 2.10. Comparison of infant hand mass as a percentage of forelimb mass to adult primates.

		Galago	*Perodicticus*	*Nycticebus*	*Ateles*	*Cebus*	*Aotus*	*Alouatta*	*Macaca*	*Papio*
	Mean	15	17.4	16.6	17	15.4	17.5	20.7	10.8	7.52
	95% CI	14.56-15.34	16.12-18.75	13.49-19.66	12.81-21.18	13.42-17.42	16.7-18.31	18.19-23.21	9.91-11.75	6.71-8.34
Age months	Hand Mass									
0.73	27.1	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.00	26.3	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.43	28	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.47	27.7	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.83	24.6	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.97	25	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.07	26.1	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.10	23.5	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.30	24.5	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.33	22.4	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.53	28.1	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.57	25.2	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.80	23.8	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.93	22.9	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.97	20	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.00	22.5	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.23	20.9	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.27	22.9	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.47	18.1	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	**Higher**
3.50	22.8	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.57	20.8	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.60	18.2	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	**Higher**
3.73	24.2	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.93	21.9	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
4.20	22.4	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
4.40	22	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
4.50	22.5	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
4.53	17.2	**Higher**	*Equal*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
4.67	22.5	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
5.03	20.1	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
5.07	14.9	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	**Higher**	**Higher**
5.50	19.3	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
5.53	17.6	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	**Higher**
5.53	19.5	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
5.77	19.8	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
5.80	17.6	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	**Higher**
6.03	21.5	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
6.13	23.5	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.17	17.7	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	**Higher**
6.23	20.3	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
6.50	19.2	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
6.70	15.1	*Equal*	*Lower*	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	**Higher**	**Higher**
6.97	19.9	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
7.17	19	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
7.37	18.4	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
7.40	18.5	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
7.43	19.5	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
8.10	17.4	**Higher**	*Equal*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
8.13	18.4	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
9.00	19	**Higher**	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
9.03	18.4	**Higher**	*Equal*	*Equal*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**

Table 2.11. Comparison of infant thigh mass as a percentage of hindlimb mass to adult primates.

		Galago	*Perodicticus*	*Nycticebus*	*Ateles*	*Cebus*	*Aotus*	*Alouatta*	*Macaca*	*Papio*
	Mean	67.30	45.56	49.53	55.26	55.20	59.11	65.46	65.38	71.25
	95% CI	65.41-69.19	43.66-47.46	43.67-55.4	50-60.52	51.46-58.95	55.8-62.43	61.91-69	62.88-67.87	68.7-73.8
Age months	Thigh Mass									
0.73	45.60	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.00	44.78	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.43	39.12	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.47	43.08	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.83	45.53	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.97	54.93	*Lower*	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
2.07	48.51	*Lower*	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.10	49.86	*Lower*	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.30	45.72	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.33	44.59	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.53	41.74	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.57	46.60	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.80	45.74	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.93	62.11	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Equal*	*Lower*	*Lower*
2.97	51.45	*Lower*	**Higher**	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.00	44.00	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.23	46.52	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.27	49.30	*Lower*	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.47	42.39	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.50	53.04	*Lower*	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
3.57	49.01	*Lower*	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.60	52.21	*Lower*	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
3.73	51.63	*Lower*	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
3.93	46.30	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.20	52.40	*Lower*	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
4.40	50.91	*Lower*	**Higher**	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.50	53.54	*Lower*	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
4.53	57.29	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
4.67	54.48	*Lower*	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
5.03	57.53	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
5.07	61.28	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*
5.50	55.57	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
5.53	57.35	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
5.53	56.26	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
5.77	58.39	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
5.80	72.28	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*
6.03	44.53	*Lower*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.13	61.73	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*
6.17	58.90	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
6.23	57.13	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
6.50	87.97	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.70	57.23	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
6.97	56.33	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
7.17	66.71	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Equal*	*Lower*
7.37	62.76	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Lower*	*Lower*
7.40	61.35	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*
7.43	56.94	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*
8.10	64.71	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Equal*	*Lower*
8.13	63.46	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Equal*	*Lower*
9.00	55.43	*Lower*	**Higher**	**Higher**	*Equal*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*
9.03	61.12	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*

Table 2.12. Comparison of infant leg mass as a percentage of hindlimb mass to adult primates.

Age months	Leg Mass	*Galago*	*Perodicticus*	*Nycticebus*	*Ateles*	*Cebus*	*Aotus*	*Alouatta*	*Macaca*	*Papio*
	Mean	22.00	30.90	32.92	27.16	27.95	26.43	32.00	23.46	21.06
	95% CI	21.08-22.92	29.64-32.16	29.86-35.98	25.26-29.06	27.09-28.82	25.19-27.67	23.42-40.58	21.87-25.05	18.82-23.29
0.73	26.11	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
1.00	25.95	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
1.43	32.44	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
1.47	29.93	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
1.83	28.58	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**
1.97	26.52	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
2.07	26.56	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
2.10	25.80	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
2.30	25.65	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
2.33	36.37	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.53	30.13	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.57	31.69	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.80	29.59	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.93	21.97	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*
2.97	27.67	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**
3.00	29.39	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.23	28.95	**Higher**	*Lower*	*Lower*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.27	26.97	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
3.47	30.76	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.50	26.79	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
3.57	28.25	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**
3.60	28.14	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**
3.73	27.81	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**
3.93	30.36	**Higher**	*Equal*	*Equal*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
4.20	27.27	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	**Higher**	**Higher**
4.40	29.15	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
4.50	28.21	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**
4.53	23.31	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	**Higher**
4.67	26.41	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
5.03	26.76	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
5.07	24.05	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**
5.50	25.87	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
5.53	26.08	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
5.53	26.17	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
5.77	25.64	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
5.80	17.96	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.03	38.15	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
6.13	24.94	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**
6.17	26.38	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
6.23	25.94	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
6.50	7.12	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.70	24.43	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**
6.97	26.00	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
7.17	20.25	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*
7.37	23.34	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	**Higher**
7.40	24.32	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**
7.43	26.15	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**
8.10	22.85	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*
8.13	23.61	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**
9.00	29.01	**Higher**	*Lower*	*Lower*	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
9.03	23.73	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Equal*	**Higher**

Table 2.13. Comparison of infant foot mass as a percentage of hindlimb mass to adult primates.

Taxon		*Galago*	*Perodicticus*	*Nycticebus*	*Ateles*	*Cebus*	*Aotus*	*Alouatta*	*Macaca*	*Papio*
Mean		10.71	23.54	17.55	17.58	16.84	14.46	25.81	11.16	7.69
95% CI		9.74-11.68	21.21-25.87	14.07-21.02	12.57-22.6	13.12-20.56	12.34-16.57	21.88-29.73	9.52-12.81	6.59-8.79
Age months	Foot Mass									
0.73	28.29	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
1.00	29.27	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
1.43	28.44	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
1.47	26.99	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
1.83	25.89	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
1.97	18.55	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
2.07	24.92	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.10	24.34	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.30	28.63	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.33	19.03	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
2.53	28.12	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.57	21.71	**Higher**	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**
2.80	24.67	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
2.93	15.92	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
2.97	20.88	**Higher**	*Lower*	*Equal*	*Equal*	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**
3.00	26.60	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.23	24.53	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.27	23.73	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.47	26.84	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.50	20.17	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
3.57	22.73	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
3.60	19.64	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
3.73	20.56	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
3.93	23.34	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
4.20	20.33	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
4.40	19.94	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
4.50	18.25	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
4.53	19.40	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
4.67	19.11	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
5.03	15.71	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
5.07	14.67	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
5.50	18.56	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
5.53	16.56	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
5.53	17.57	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
5.77	15.97	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
5.80	9.76	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	**Higher**
6.03	17.32	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
6.13	13.33	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
6.17	14.72	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
6.23	16.93	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
6.50	4.91	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.70	18.35	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
6.97	17.67	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
7.17	13.04	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	**Higher**	**Higher**
7.37	13.91	**Higher**	*Lower*	*Lower*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
7.40	14.33	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
7.43	16.91	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**
8.10	12.44	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	**Higher**
8.13	12.93	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	**Higher**	**Higher**
9.00	15.57	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**
9.03	15.15	**Higher**	*Lower*	*Equal*	*Equal*	*Equal*	*Equal*	*Lower*	**Higher**	**Higher**

Table 2.14. Comparison of infant arm mass as a percentage of forelimb mass to non-primates.

		Tupaia	*Marmosa*	*Philander*	*Didelphis*	*Caluromys*	*Monodelphis*	*Metachirus*	*Felis*	*Canis*	*Equis*
	Mean	62.71	52.85	50.98	47.93	46.97	54.74	56.86	57.53	62.72	72.46
	95% CI	58.99-66.44		48.78-53.18		43.59-50.35			57.15-57.91	60.53-64.9	
Age months	Arm Mass										
0.73	35.58	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.00	33.96	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.43	33.94	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.47	37.13	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.83	39.29	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.97	37.99	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.07	38.20	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.10	42.90	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.30	42.04	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.33	40.18	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.53	38.02	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.57	39.04	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.80	38.87	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.93	38.98	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.97	40.56	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.00	43.87	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.23	43.31	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.27	40.67	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.47	40.95	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.50	36.46	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.57	40.53	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.60	44.48	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.73	36.43	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.93	40.21	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.20	40.24	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.40	40.59	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.50	40.19	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.53	44.40	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.67	38.81	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.03	43.93	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.07	50.29	*Lower*	*Lower*	*Equal*	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.50	44.10	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.53	47.03	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.53	47.05	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.77	40.91	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.80	46.04	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.03	39.39	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.13	42.29	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.17	42.54	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.23	39.02	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.50	44.82	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.70	51.18	*Lower*	*Lower*	*Equal*	**Higher**	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.97	42.65	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
7.17	42.19	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
7.37	45.95	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
7.40	44.66	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
7.43	44.23	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
8.10	44.78	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
8.13	38.83	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
9.00	43.94	*Lower*	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
9.03	43.22	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*

Table 2.14. Comparison of forearm mass as a percentage of forelimb mass to non-primates.

Age months	FA % FM	*Tupaia*	*Marmosa*	*Philander*	*Didelphis*	*Caluromys*	*Monodelphis*	*Metachirus*	*Felis*	*Canis*	*Equis*
	Mean	28.35	36.94	36.39	34.46	40.44	36.21	31.44	30.90	25.42	18.36
	95% CI	26.01-30.7		34.96-37.81		37.59-43.29			30.26-31.54	24.09-26.74	
0.73	37.36	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.00	39.72	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.43	38.02	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.47	35.21	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
1.83	36.15	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
1.97	37.03	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.07	35.66	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
2.10	33.63	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
2.30	33.44	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
2.33	37.38	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.53	33.92	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
2.57	35.72	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
2.80	37.35	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.93	38.09	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.97	39.40	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.00	33.60	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
3.23	35.75	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
3.27	36.44	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.47	40.92	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.50	40.73	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.57	38.68	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.60	37.34	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.73	39.42	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.93	37.94	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.20	37.38	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.40	37.46	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.50	37.31	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.53	38.43	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.67	38.66	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.03	35.98	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
5.07	34.77	**Higher**	*Lower*	*Lower*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
5.50	36.63	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.53	35.37	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
5.53	33.47	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
5.77	39.31	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.80	36.33	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.03	39.13	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.13	34.16	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
6.17	39.77	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.23	40.69	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.50	35.95	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
6.70	33.69	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
6.97	37.47	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.17	38.80	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.37	35.63	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**
7.40	36.83	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.43	36.28	**Higher**	*Lower*	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
8.10	37.87	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
8.13	42.75	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.00	37.09	**Higher**	**Higher**	*Equal*	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.03	38.36	**Higher**	**Higher**	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**

Table 2.15. Comparison of infant hand mass as a percentage of forelimb mass to non-primates.

		Tupaia	*Marmosa*	*Philander*	*Didelphis*	*Caluromys*	*Monodelphis*	*Metachirus*	*Felis*	*Canis*	*Equis*
	Mean	8.93	10.21	12.64	17.61	12.59	9.05	11.70	11.57	11.87	9.18
	95% CI	6.49-11.38		11.72-13.56		11.39-13.78			11.19-11.95	10.99-12.75	
Age months	Hand % FM										
0.73	27.06	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.00	26.31	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.43	28.04	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.47	27.66	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.83	24.56	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.97	24.98	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.07	26.14	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.10	23.47	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.30	24.52	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.33	22.45	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.53	28.06	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.57	25.24	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.80	23.78	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.93	22.93	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.97	20.04	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.00	22.53	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.23	20.94	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.27	22.89	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.47	18.13	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.50	22.81	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.57	20.79	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.60	18.18	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.73	24.15	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.93	21.86	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.20	22.38	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.40	21.95	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.50	22.51	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.53	17.17	**Higher**	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.67	22.53	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.03	20.09	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.07	14.94	**Higher**	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.50	19.28	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.53	17.60	**Higher**	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.53	19.48	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.77	19.78	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.80	17.63	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.03	21.48	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.13	23.54	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.17	17.69	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.23	20.28	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.50	19.24	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.70	15.12	**Higher**	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.97	19.88	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.17	19.01	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.37	18.43	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.40	18.51	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.43	19.49	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
8.10	17.35	**Higher**	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
8.13	18.42	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.00	18.97	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.03	18.42	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**

Table 2.16. Comparison of infant thigh mass as a percentage of hindlimb mass to non-primates.

		Tupaia	*Marmosa*	*Philander*	*Didelphis*	*Caluromys*	*Monodelphis*	*Metachirus*	*Felis*	*Canis*	*Equis*
	Mean	70.37	62.30	66.08	63.22	64.66	68.14	70.51	66.22	76.73	76.14
	95% CI	69.74-70.99		65.08-67.07		62.78-66.55			64.77-67.66	75.77-77.68	
Age months	Thigh % HM										
0.73	45.60	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.00	44.78	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.43	39.12	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.47	43.08	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.83	45.53	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
1.97	54.93	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.07	48.51	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.10	49.86	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.30	45.72	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.33	44.59	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.53	41.74	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.57	46.60	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.80	45.74	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.93	62.11	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
2.97	51.45	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.00	44.00	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.23	46.52	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.27	49.30	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.47	42.39	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.50	53.04	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.57	49.01	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.60	52.21	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.73	51.63	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
3.93	46.30	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.20	52.40	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.40	50.91	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.50	53.54	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.53	57.29	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
4.67	54.48	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.03	57.53	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.07	61.28	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.50	55.57	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.53	57.35	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.53	56.26	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.77	58.39	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
5.80	72.28	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	*Lower*	*Lower*
6.03	44.53	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.13	61.73	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.17	58.90	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.23	57.13	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.50	87.97	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.70	57.23	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.97	56.33	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
7.17	66.71	*Lower*	**Higher**	*Equal*	**Higher**	**Higher**	*Lower*	*Lower*	*Equal*	*Lower*	*Lower*
7.37	62.76	*Lower*	**Higher**	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
7.40	61.35	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
7.43	56.94	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
8.10	64.71	*Lower*	**Higher**	*Lower*	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
8.13	63.46	*Lower*	**Higher**	*Lower*	**Higher**	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
9.00	55.43	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
9.03	61.12	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*

Table 2.17. Comparison of infant leg mass as a percentage of hindlimb mass to non-primates.

		Tupaia	*Marmosa*	*Philander*	*Didelphis*	*Caluromys*	*Monodelphis*	*Metachirus*	*Felis*	*Canis*	*Equis*
	Mean	21.88	27.23	24.11	23.88	24.59	24.19	21.58	24.40	16.53	14.70
	95% CI	20.66-23.1		23.54-24.69		23.23-25.95			24.15-24.64	16.05-17.01	
Age months	Leg Mass										
0.73	26.11	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.00	25.95	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.43	32.44	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.47	29.93	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.83	28.58	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.97	26.52	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.07	26.56	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.10	25.80	**Higher**	*Lower*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.30	25.65	**Higher**	*Lower*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.33	36.37	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.53	30.13	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.57	31.69	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.80	29.59	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.93	21.97	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	*Lower*	**Higher**	**Higher**
2.97	27.67	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.00	29.39	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.23	28.95	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.27	26.97	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.47	30.76	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.50	26.79	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.57	28.25	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.60	28.14	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.73	27.81	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.93	30.36	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.20	27.27	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.40	29.15	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.50	28.21	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.53	23.31	**Higher**	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	**Higher**	*Lower*	**Higher**	**Higher**
4.67	26.41	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.03	26.76	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.07	24.05	**Higher**	*Lower*	*Equal*	**Higher**	*Equal*	*Lower*	**Higher**	*Lower*	**Higher**	**Higher**
5.50	25.87	**Higher**	*Lower*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.53	26.08	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.53	26.17	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.77	25.64	**Higher**	*Lower*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.80	17.96	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**
6.03	38.15	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.13	24.94	**Higher**	*Lower*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.17	26.38	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.23	25.94	**Higher**	*Lower*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.50	7.12	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.70	24.43	**Higher**	*Lower*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
6.97	26.00	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.17	20.25	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	**Higher**
7.37	23.34	**Higher**	*Lower*	*Lower*	*Lower*	*Equal*	*Lower*	**Higher**	*Lower*	**Higher**	**Higher**
7.40	24.32	**Higher**	*Lower*	*Equal*	**Higher**	*Equal*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
7.43	26.15	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
8.10	22.85	*Equal*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	**Higher**	*Lower*	**Higher**	**Higher**
8.13	23.61	**Higher**	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	**Higher**	*Lower*	**Higher**	**Higher**
9.00	29.01	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.03	23.73	**Higher**	*Lower*	*Equal*	*Lower*	*Equal*	*Lower*	**Higher**	*Lower*	**Higher**	**Higher**

Table 2.18. Comparison of infant foot mass as a percentage of hindlimb mass to non-primates.

		Tupaia	*Marmosa*	*Philander*	*Didelphis*	*Caluromys*	*Monodelphis*	*Metachirus*	*Felis*	*Canis*	*Equis*
Mean		7.75	10.47	9.81	12.90	10.75	7.67	7.91	9.39	6.74	9.16
95% CI		6.45-9.05		9.18-10.45		10.21-11.28			8.13-10.64	6.24-7.25	
Age months	Foot Mass										
0.73	28.29	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.00	29.27	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.43	28.44	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.47	26.99	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.83	25.89	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
1.97	18.55	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.07	24.92	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.10	24.34	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.30	28.63	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.33	19.03	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.53	28.12	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.57	21.71	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.80	24.67	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.93	15.92	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
2.97	20.88	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.00	26.60	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.23	24.53	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.27	23.73	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.47	26.84	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.50	20.17	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.57	22.73	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.60	19.64	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.73	20.56	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
3.93	23.34	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.20	20.33	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.40	19.94	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.50	18.25	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.53	19.40	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
4.67	19.11	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.03	15.71	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.07	14.67	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.50	18.56	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.53	16.56	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.53	17.57	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.77	15.97	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
5.80	9.76	**Higher**	*Lower*	*Equal*	*Lower*	*Lower*	**Higher**	**Higher**	*Equal*	**Higher**	**Higher**
6.03	17.32	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.13	13.33	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.17	14.72	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.23	16.93	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.50	4.91	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*	*Lower*
6.70	18.35	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
6.97	17.67	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.17	13.04	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.37	13.91	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.40	14.33	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
7.43	16.91	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
8.10	12.44	**Higher**	**Higher**	**Higher**	*Lower*	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
8.13	12.93	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.00	15.57	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**
9.03	15.15	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**	**Higher**

FIGURES

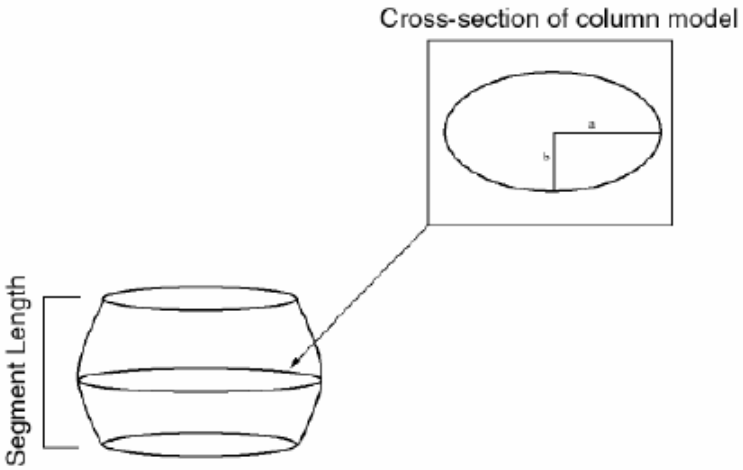


Figure 2.1 Elliptical column model (after Crompton et al., 1996).

Inset is a cross-section of the column where a and b are the lengths of the major and minor axes respectively. The model pictured is the general elliptical model. In the model used for the infant baboons, a and b are equal, making the cross-section a circle, and are used to generate segment inertial properties using equations developed in the appendix.

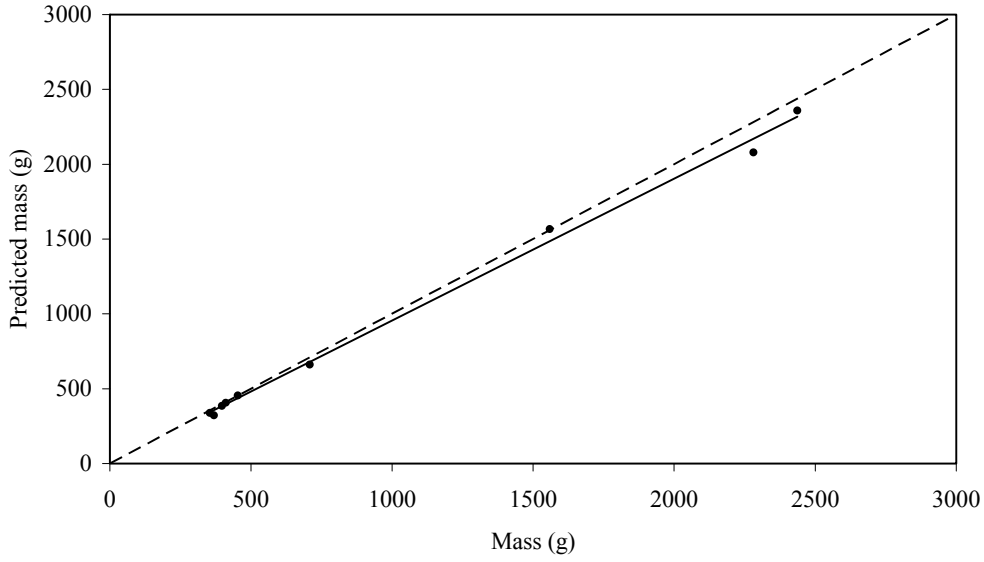


Figure 2.2a. Predicted vs. measured mass in a sample of cadaver limbs and limb segments. The dashed line is the line of identity and the solid line is a least-squares regression (r = .998, Slope (95% C.I.) = .95 (.10), Intercept (95% C.I.) = 7.216 (107.034), p<.0001).

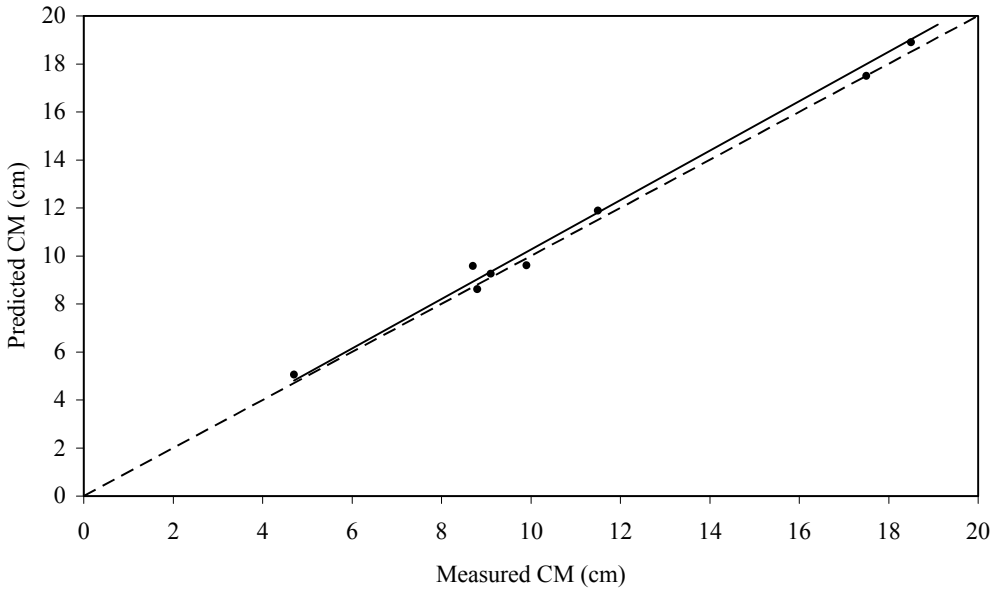


Figure 2b. Predicted vs. measured center of mass in a sample of cadaver limbs and limb segments. The dashed line is the line of identity and the solid line is a least-squares regression (r = .996, Slope (95% C.I.) = 1.03 (.08), Intercept (95% C.I.) = .03 (1.03), $p<.0001$).

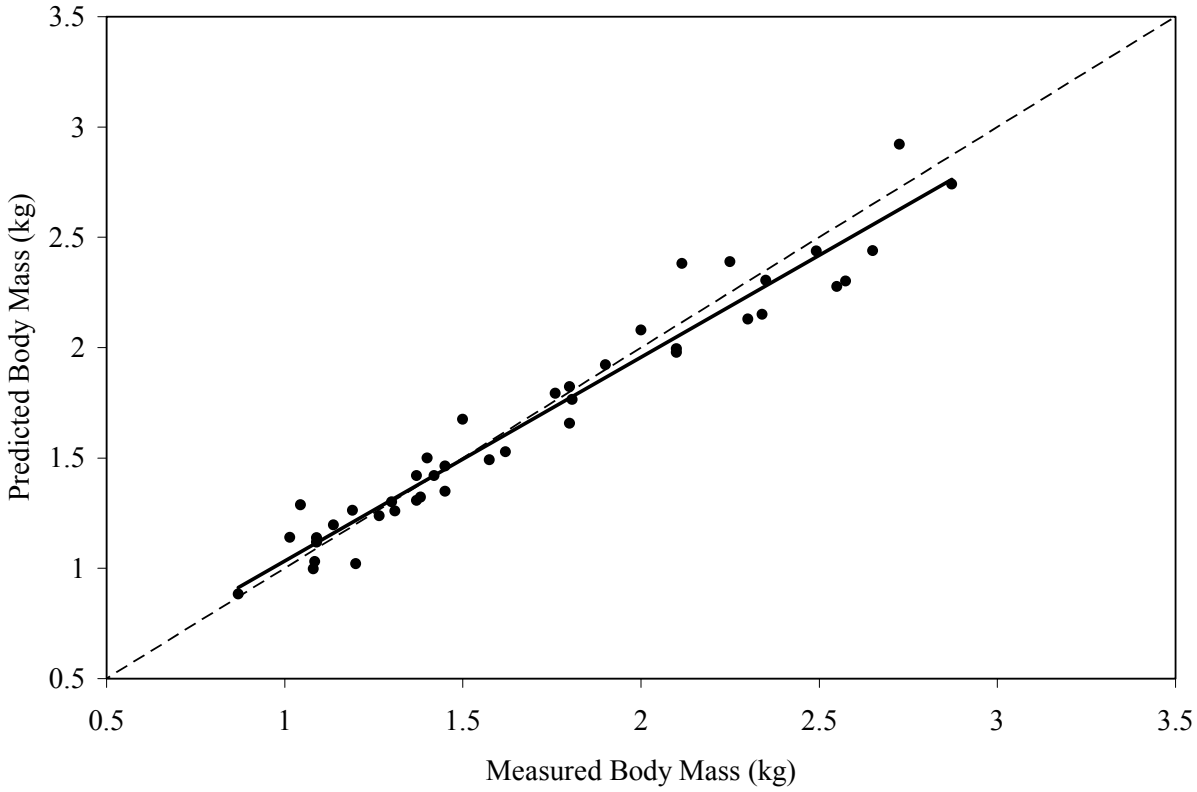


Figure 2.2c. Predicted vs. measured body masses in the infant baboon sample.

Dotted line is the line of identity; solid line is a least squares regression line through the infant baboon sample (r = .949, Slope (95% C.I.) = .92 (.08), Intercept (95% C.I.) = .11 (.12), p<.0001)

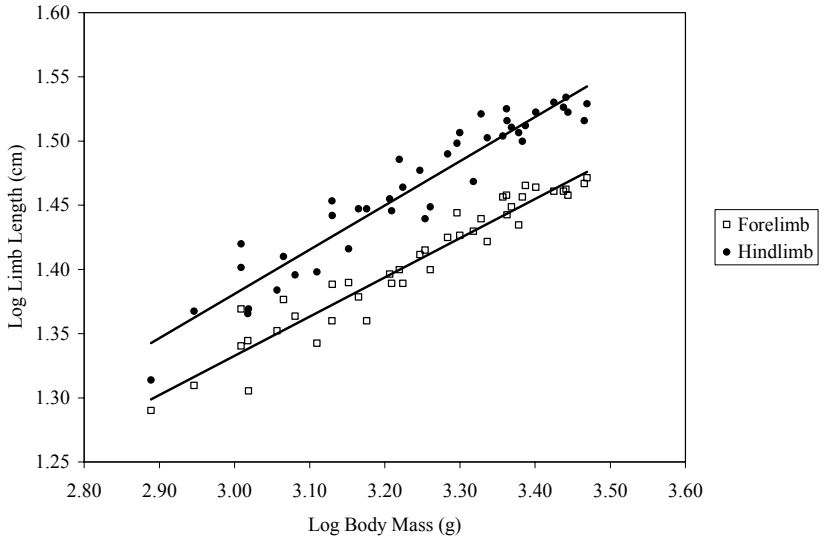


Figure 2.3. Forelimb and hindlimb length vs. body mass (values are logged) in the infant baboon sample. Open squares are hindlimb values, closed circles are forelimb values. The reduced major axis regression equations, the 95% confidence limits for the slopes and intercepts, and the correlation coefficients are listed in Table 2.2.

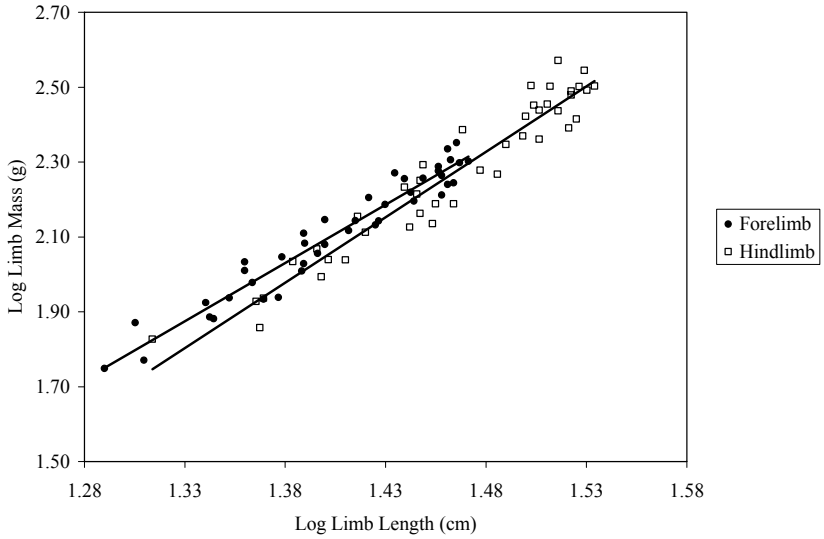


Figure 2.4. Forelimb and hindlimb mass vs. limb length (values are logged) in the infant baboon sample. Open squares are hindlimb values, closed circles are forelimb values. The reduced major axis regression equations, the 95% confidence limits for the slopes and intercepts, and the correlation coefficients are listed in Table 2.2.

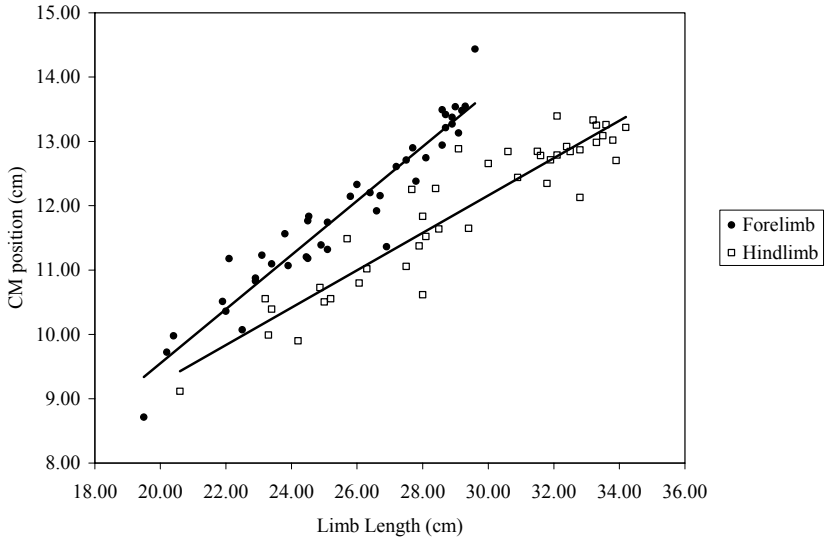


Figure 2.5. Forelimb and hindlimb CM vs. relevant limb length in the infant baboon sample. Open squares are hindlimb values, closed circles are forelimb values. The reduced major axis regression equations, the 95% confidence limits for the slopes and intercepts, and the correlation coefficients are listed in Table 2.2. Note that values are not logged.

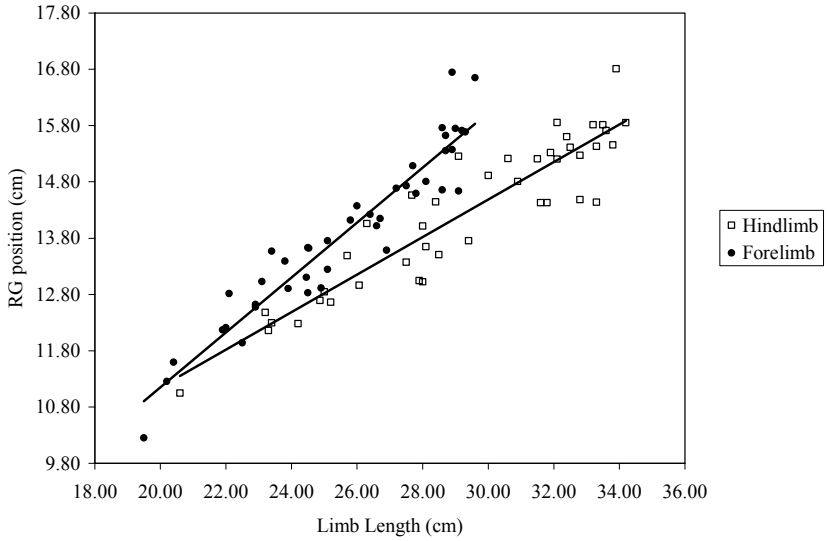


Figure 2.6. Forelimb and hindlimb RG vs. relevant limb length in the infant baboon sample. Open squares are hindlimb values, closed circles are forelimb values. The reduced major axis regression equations, the 95% confidence limits for the slopes and intercepts, and the correlation coefficients are listed in Table 2.2. Note values are not logged.

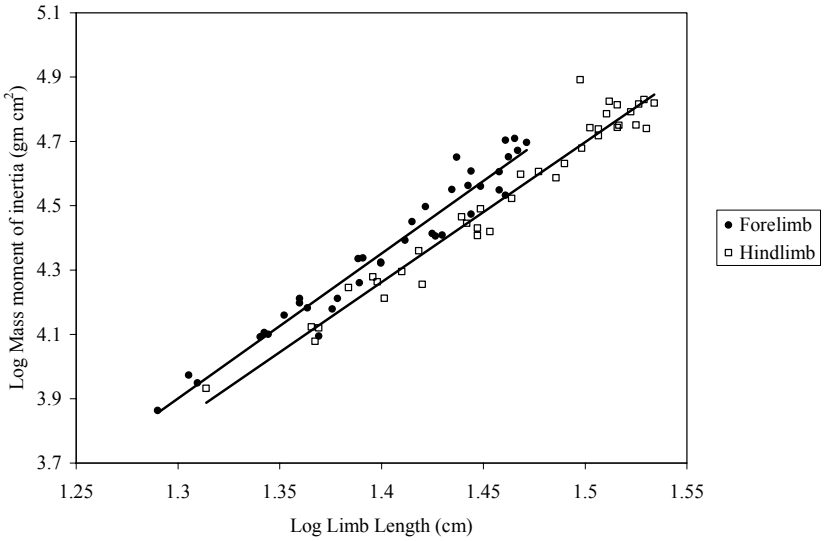


Figure 2.7. Forelimb and hindlimb mass moment of inertia vs. limb length (values are logged) in the infant baboon sample. Open squares are hindlimb values, closed circles are forelimb values. The reduced major axis regression equations, the 95% confidence limits for the slopes and intercepts, and the correlation coefficients are listed in Table 2.2.

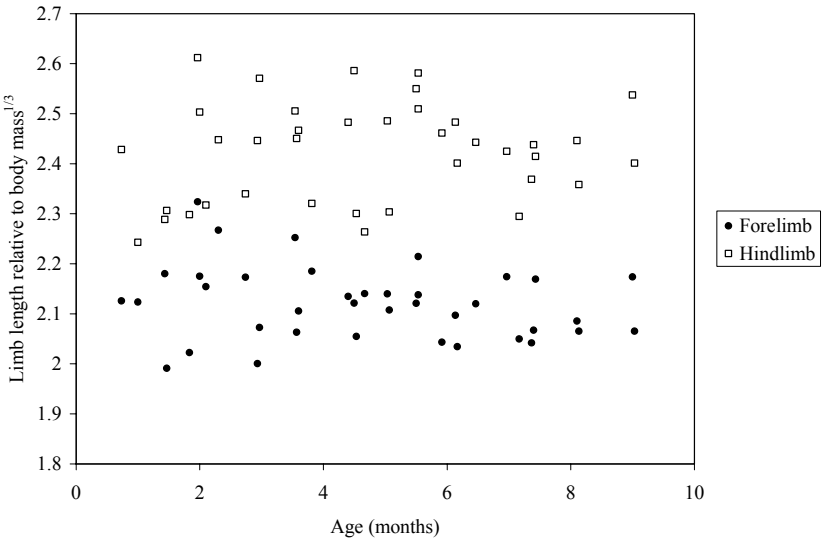


Figure 2.8. Forelimb and hindlimb length relative to the cube root of body mass vs. age in the infant baboon sample. Forelimb values are closed circles and hindlimb values are open squares. Values for the correlation coefficient and its significance can be found in Table 2.4.

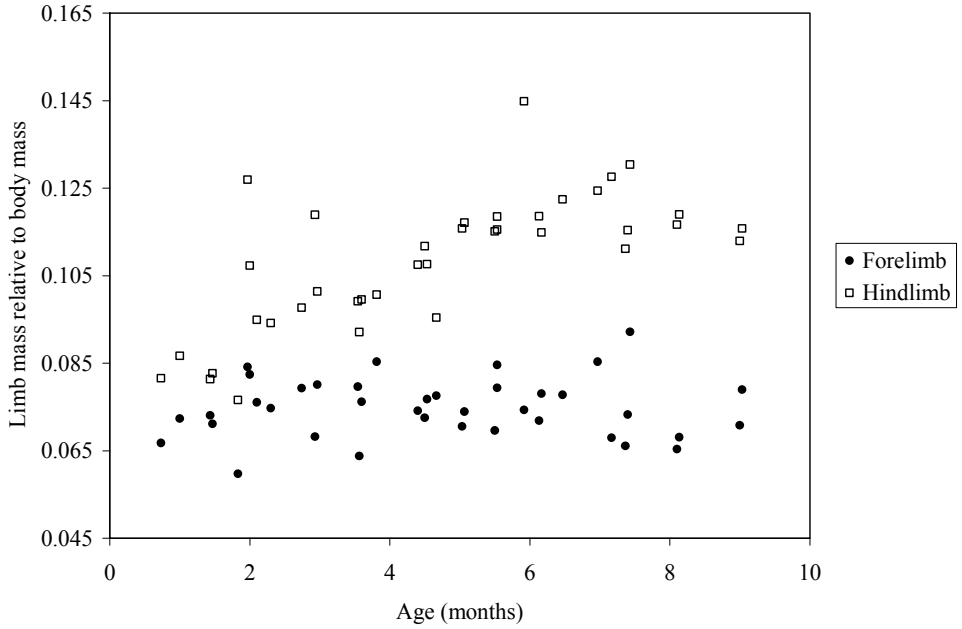


Figure 2.9. Forelimb and hindlimb mass relative to body mass vs. age in the infant baboon sample. Forelimb values are closed circles and hindlimb values are open squares. Values for the correlation coefficient and its significance can be found in table 2.4.

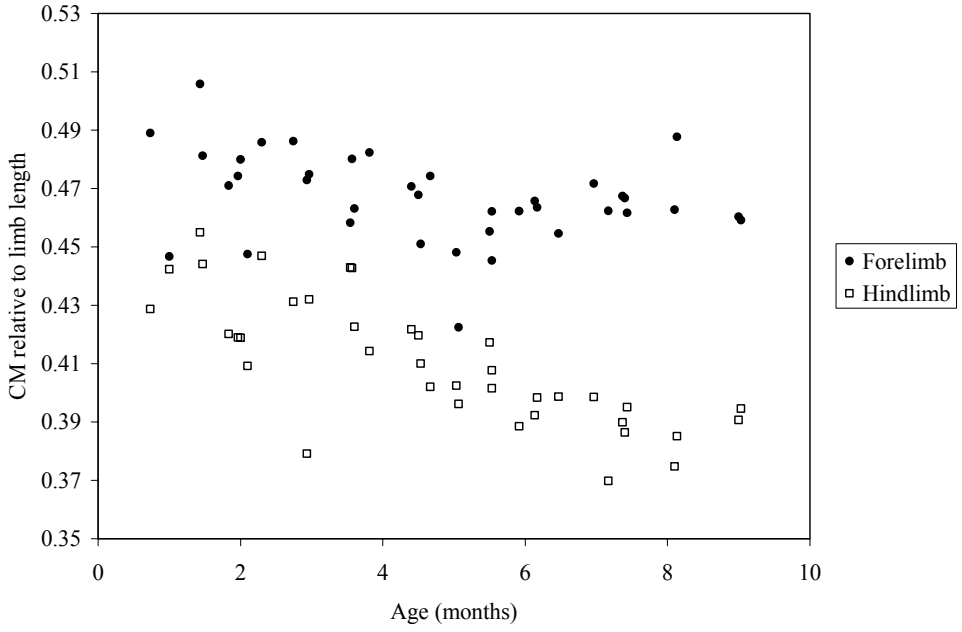


Figure 2.10. Forelimb and hindlimb CM relative to limb length vs. age in the infant baboon sample. Forelimb values are closed circles and hindlimb values are open squares. Values for the correlation coefficient and its significance can be found in Table 2.4.

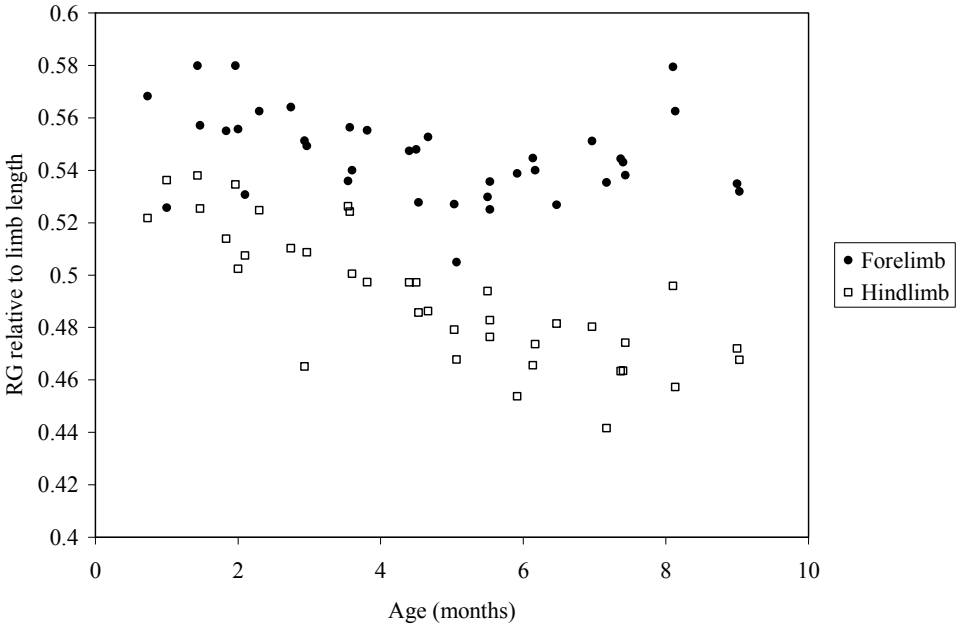


Figure 2.11. Forelimb and hindlimb RG relative to limb length vs. age in the infant baboon sample. Forelimb values are closed circles and hindlimb values are open squares. Values for the correlation coefficient and its significance can be found in Table 2.4.

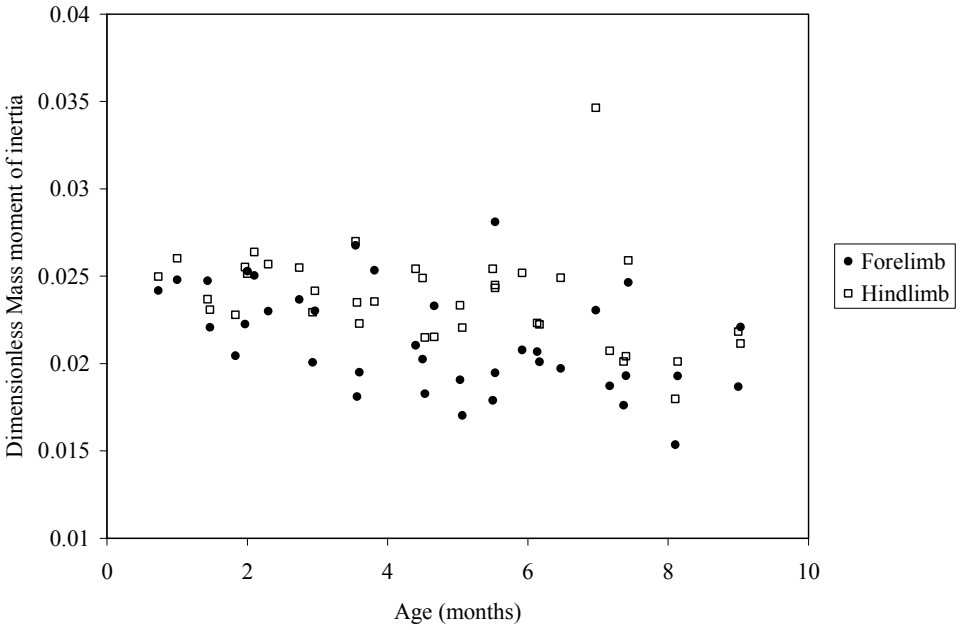


Figure 2.12. Dimensionless forelimb and hindlimb mass moment of inertia vs. age in the infant baboon sample. Forelimb values are closed circles and hindlimb values are open squares. Values for the correlation coefficient and its significance can be found in Table 2.4.

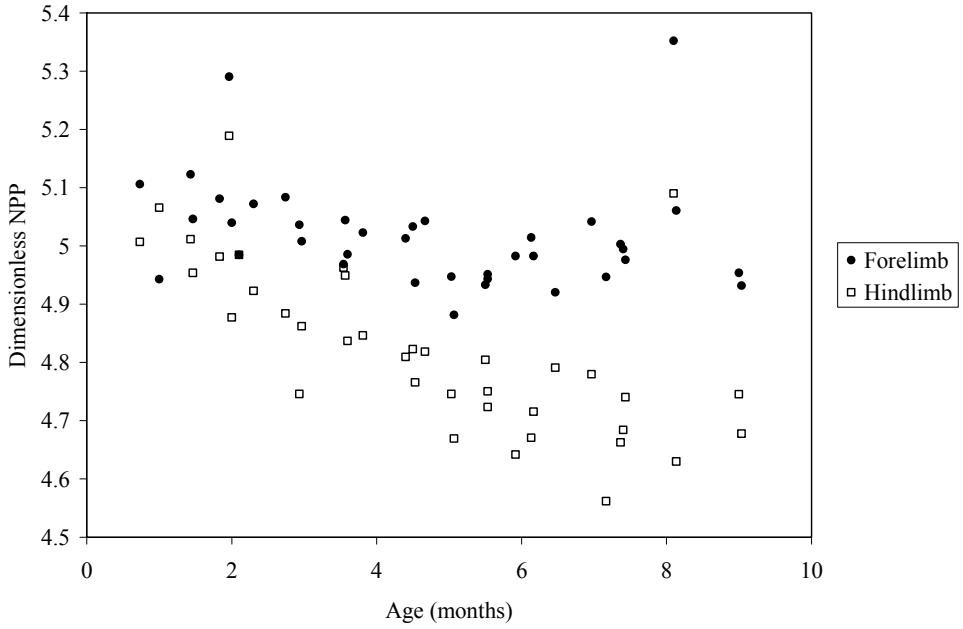


Figure 2.13. Dimensionless forelimb and hindlimb NPP vs. age in the infant baboon sample. Forelimb values are closed circles and hindlimb values are open squares. Values for the correlation coefficient and its significance can be found in Table 2.4.

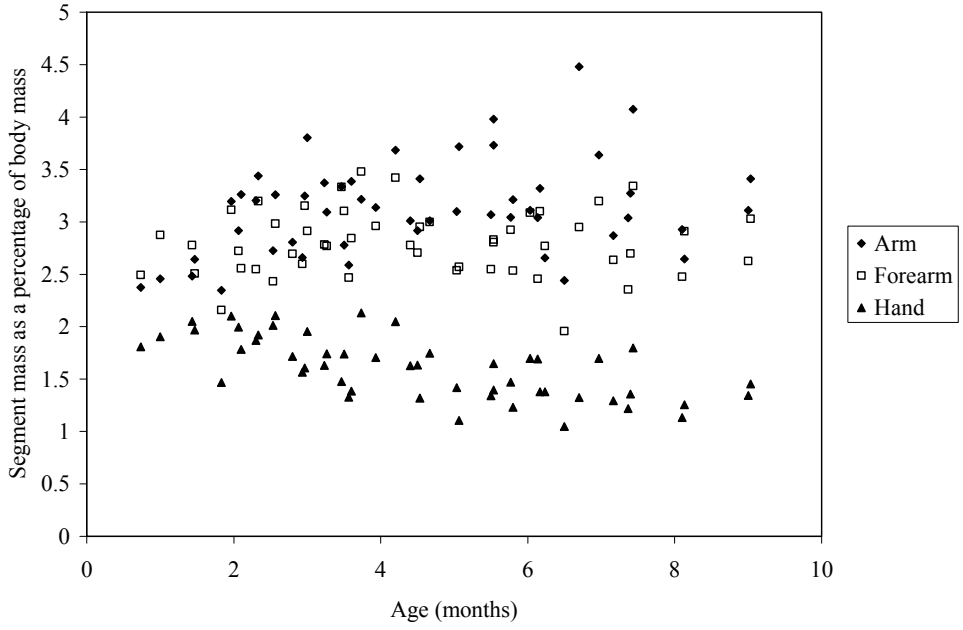


Figure 2.14. Forelimb segment masses as a percentage of body mass in the infant baboon sample. Correlation coefficients and significance can be found in Table 2.6.

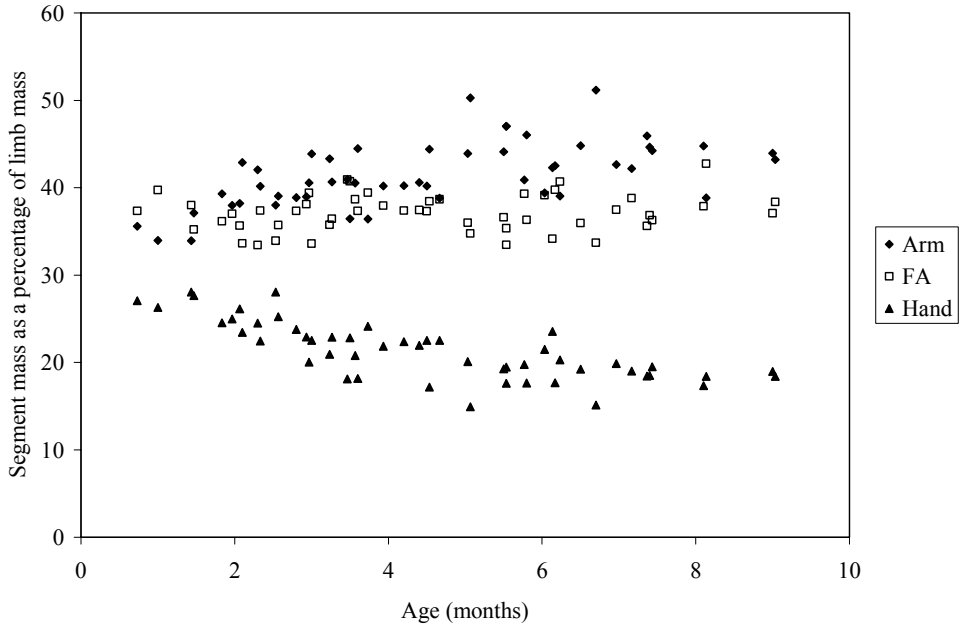


Figure 2.15. Forelimb segment masses as a percentage of forelimb mass in the infant baboon sample. Correlation coefficients and significance can be found in Table 2.6.

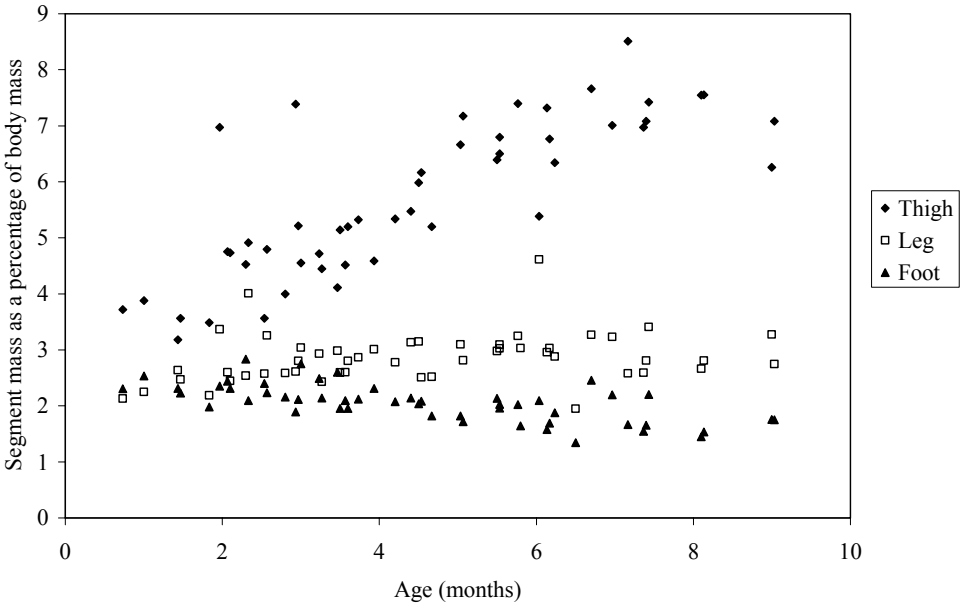


Figure 2.16. Hindlimb segment masses as a percentage of body mass in the infant baboon sample. Correlation coefficients and significance can be found in Table 2.6.

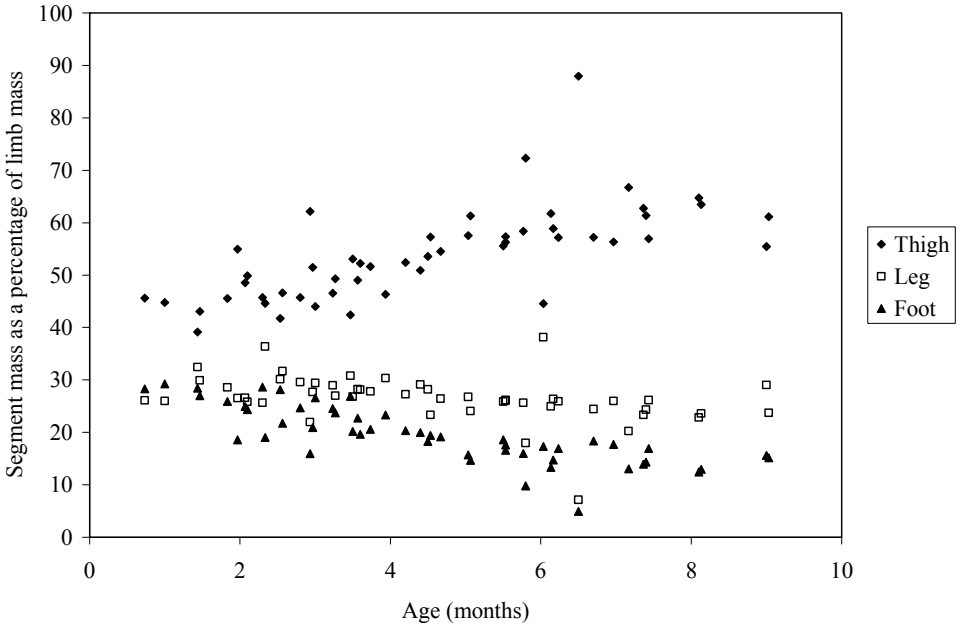


Figure 2.17. Hindlimb segment masses as a percentage of hindlimb mass in the infant baboon sample. Correlation coefficients and significance can be found in Table 2.6.

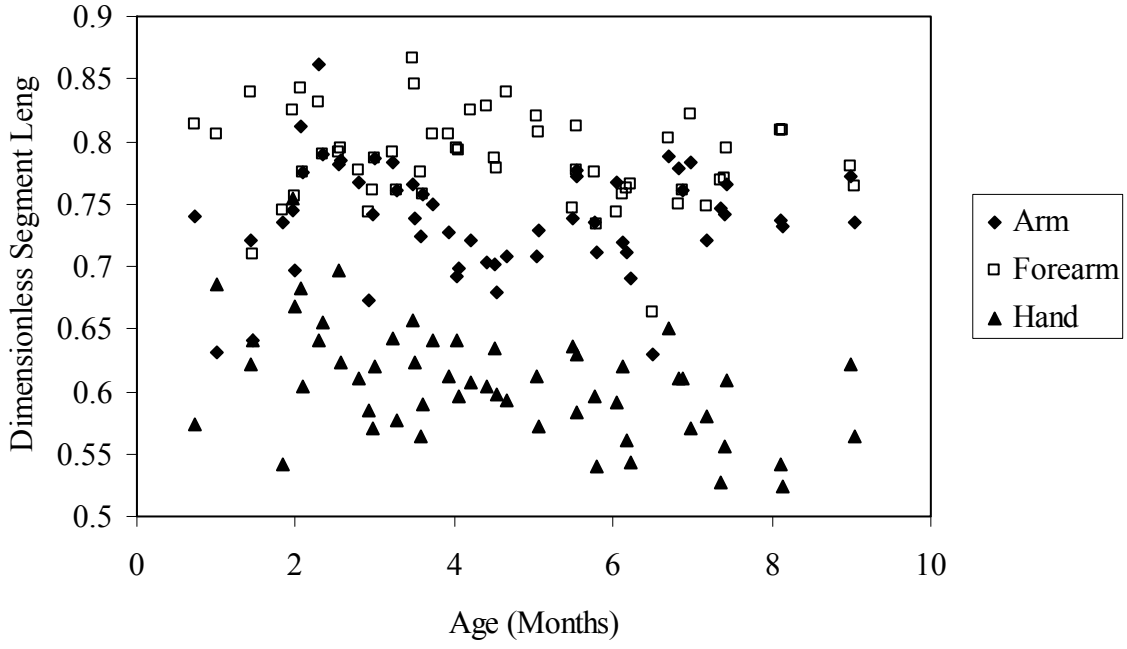


Figure 2.18. Forelimb dimensionless segment lengths in the infant baboon sample. Correlation coefficients and significance can be found in Table 2.7.

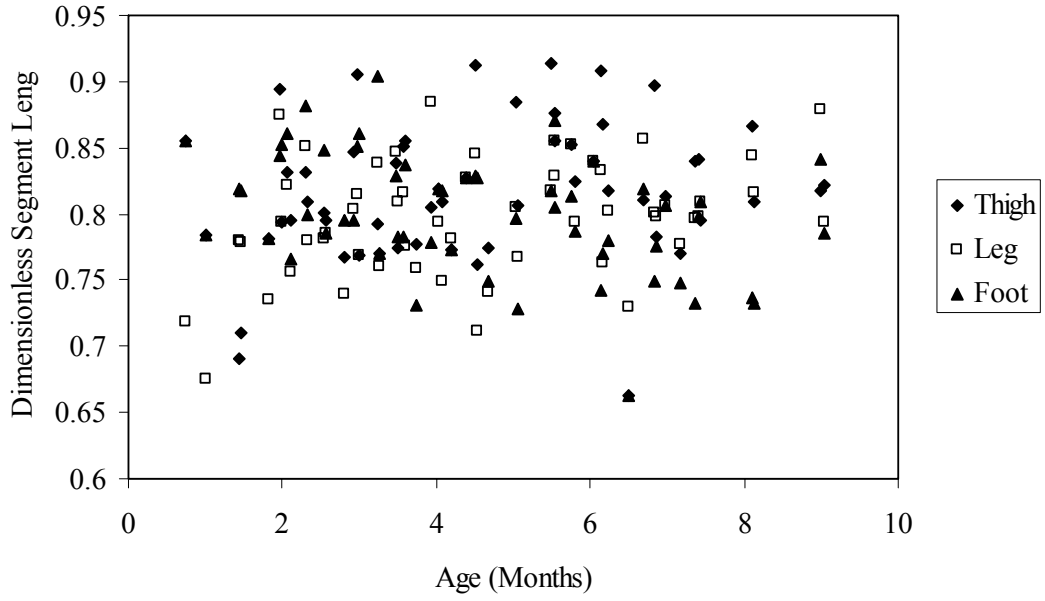


Figure 2.19. Hindlimb dimensionless segment lengths in the infant baboon sample. Correlation coefficients and significance can be found in Table 2.7.

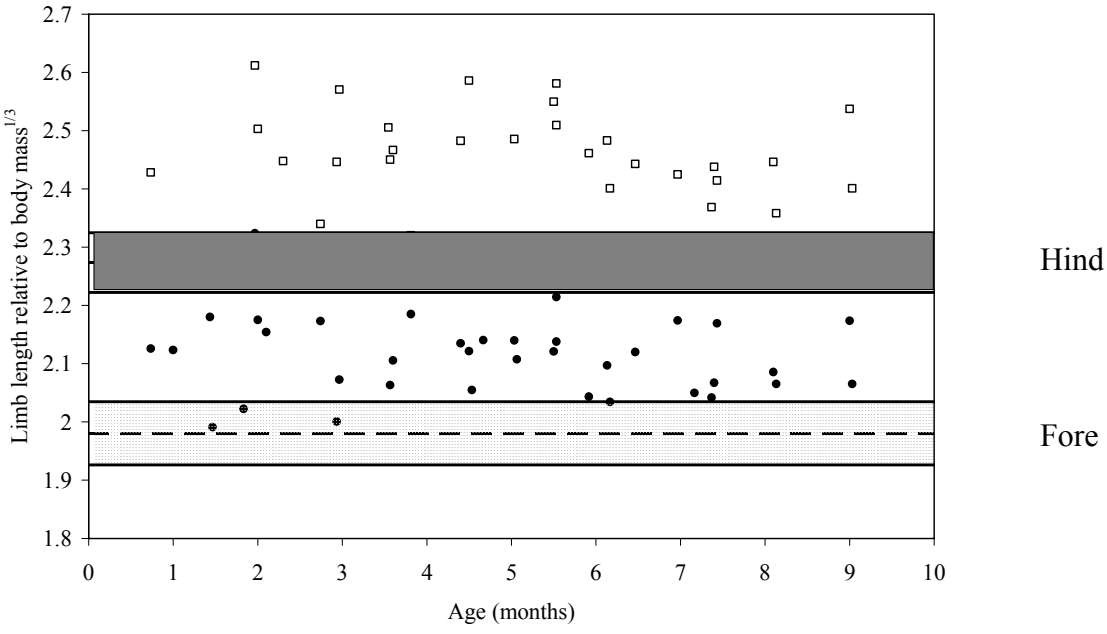


Figure 2.20. Comparison of infant baboon dimensionless limb lengths with those of adult Papio. Infant *Papio* forelimbs are closed circles and infant *Papio* hindlimbs are open squares. Adult *Papio* mean hindlimb values are indicated by the dot-dashed line and the 95% confidence limits are indicated by the solid lines above and below it, as well as the

dark grey shaded area. Adult *Papio* forelimb mean is indicated by the dashed line and the 95% confidence limits of the mean are indicated by the solid lines above and below it and the light grey shaded area.

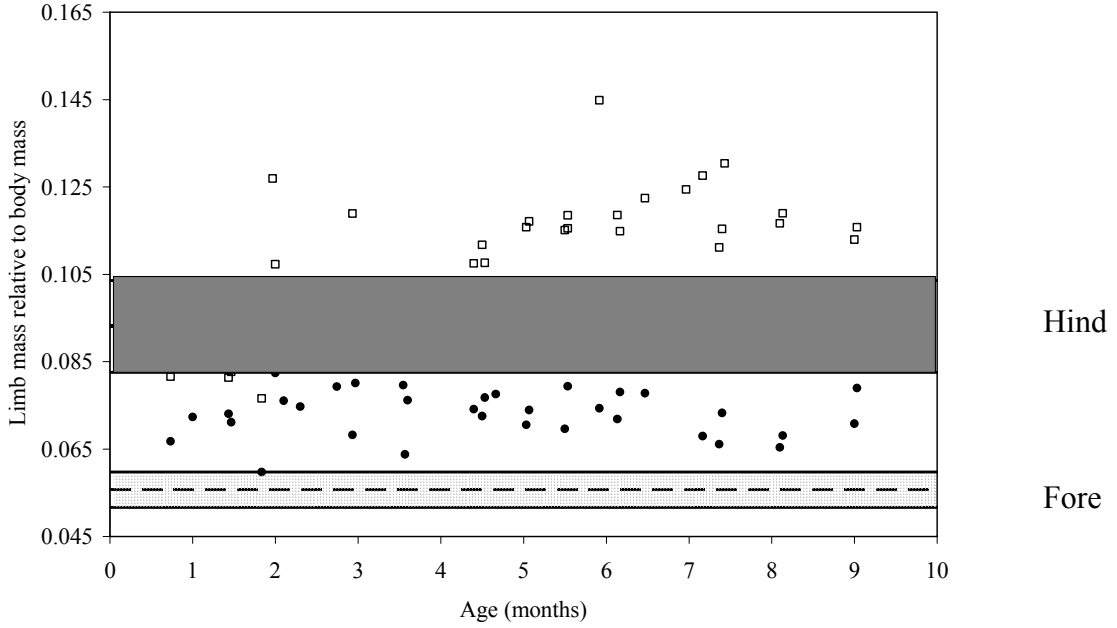


Figure 2.21. Comparison of infant baboon dimensionless limb masses with those of adult *Papio*. Symbols as in Figure 2.20.

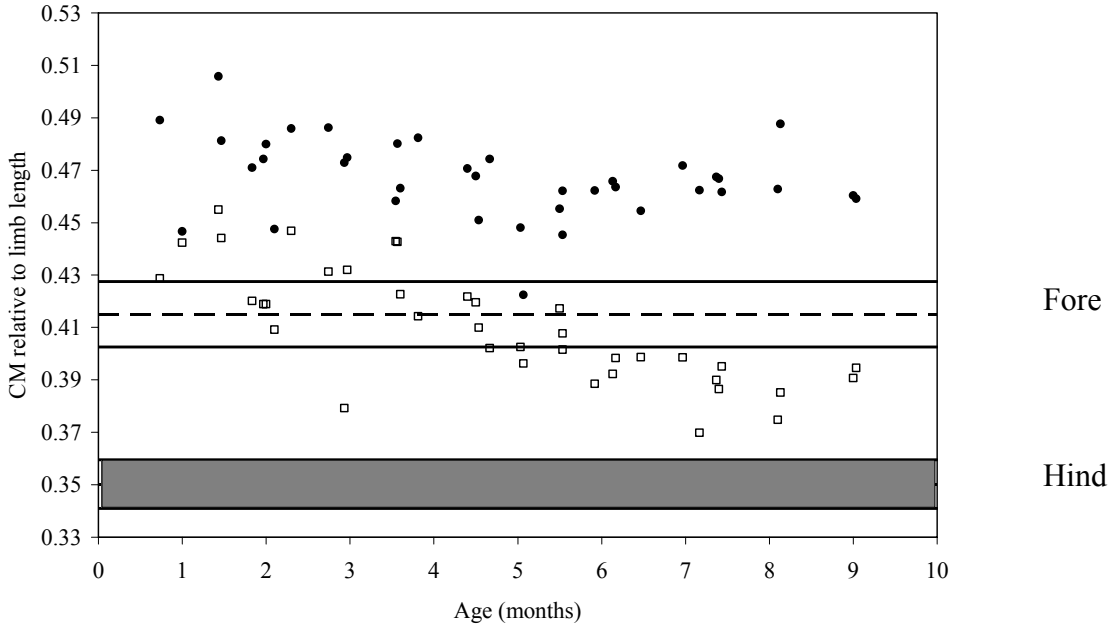


Figure 2.22. Comparison of infant baboon dimensionless limb CMs with those of adult *Papio*. Symbols as in Figure 2.20.

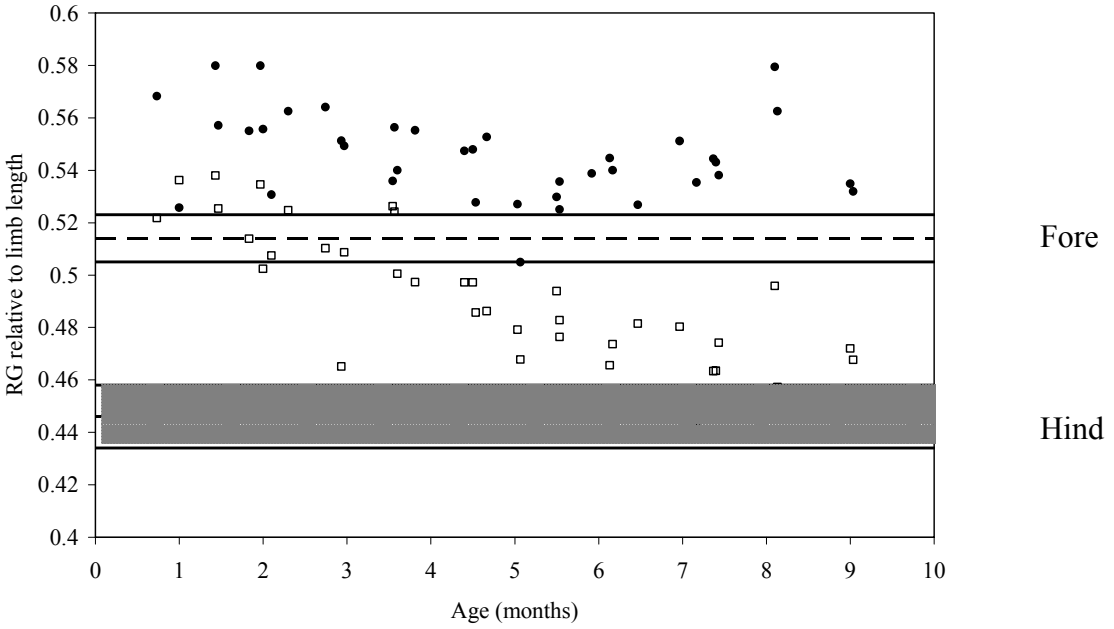


Figure 2.23. Comparison of infant baboon dimensionless limb RGs with those of adult *Papio*. Symbols as in Figure 2.20.

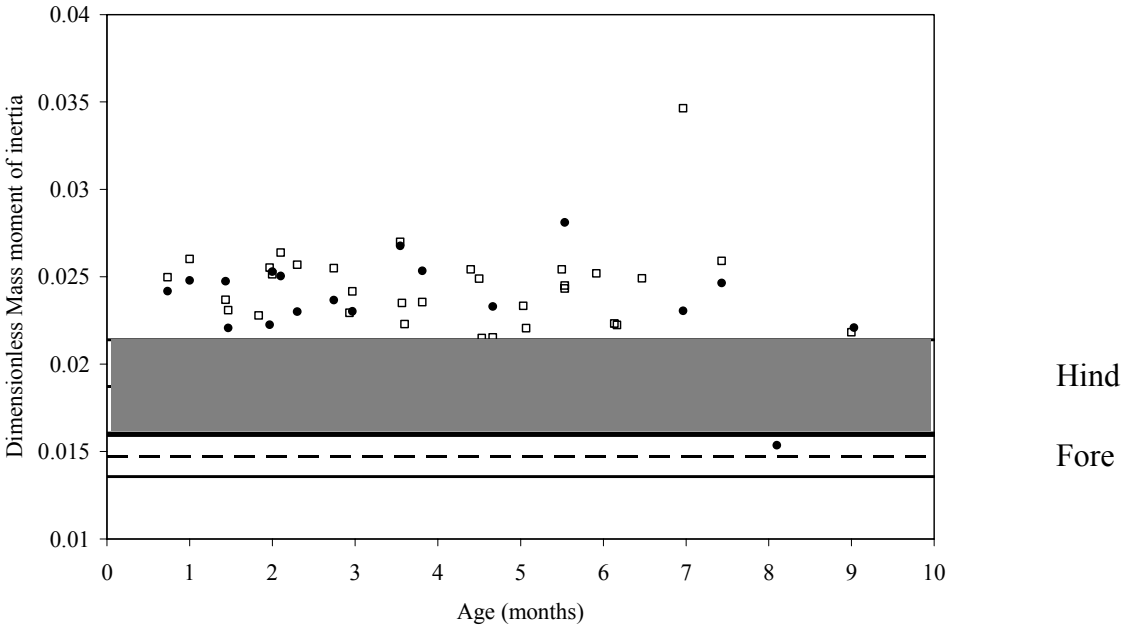


Figure 2.24. Comparison of infant baboon dimensionless limb mass moments of inertia with those of adult *Papio*. Symbols as in Figure 2.20.

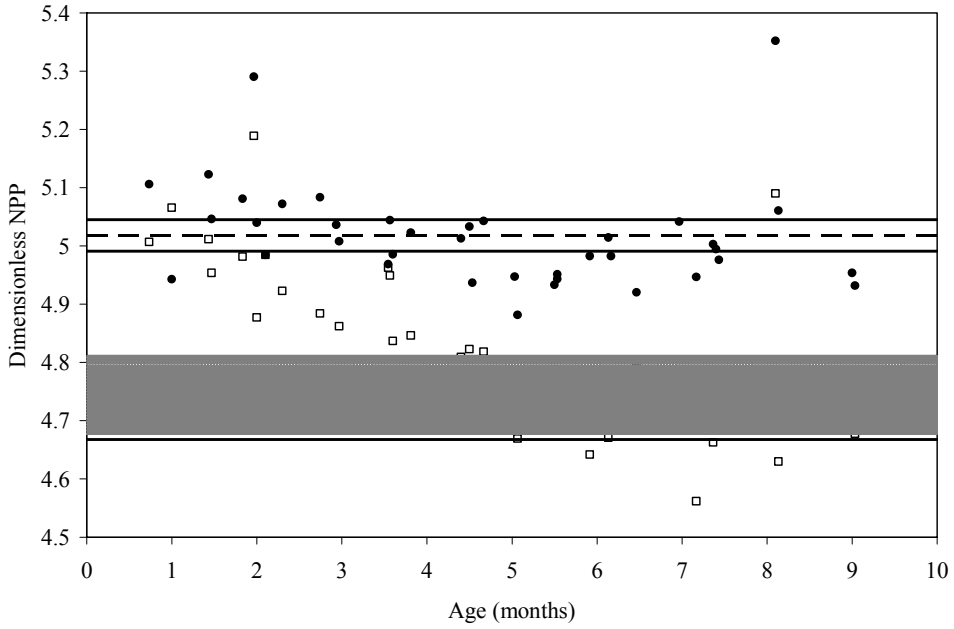


Figure 2.25. Comparison of infant baboon dimensionless limb NPPs with those of adult *Papio*. Symbols as in Figure 2.20.

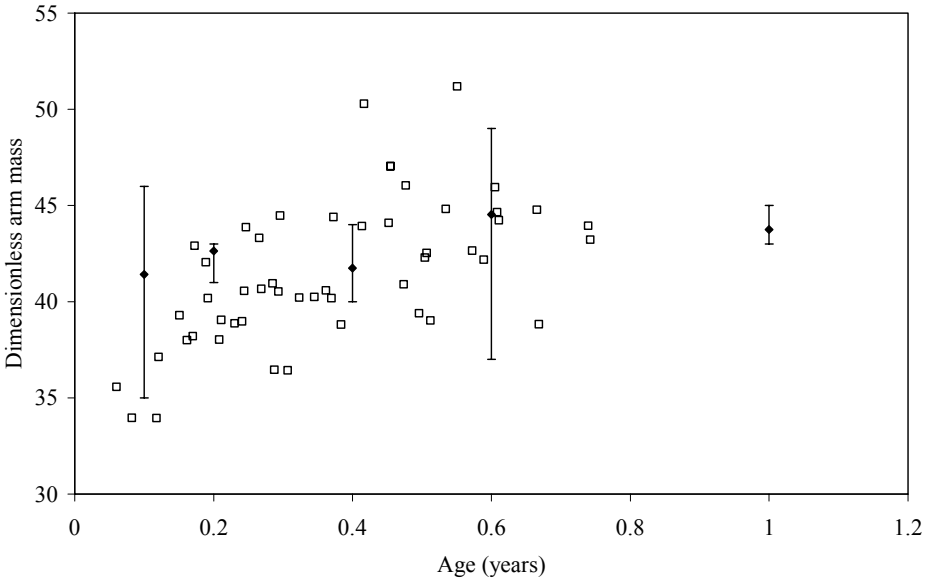


Figure 2.26. Comparison of infant baboon arm masses as a percentage of forelimb mass with those of infant *Macaca* (data from Turnquist and Wells, 1994). Infant baboon values are open squares, mean values of *Macaca* at each age are closed diamonds, bars represent the range for infant *Macaca* at each age.

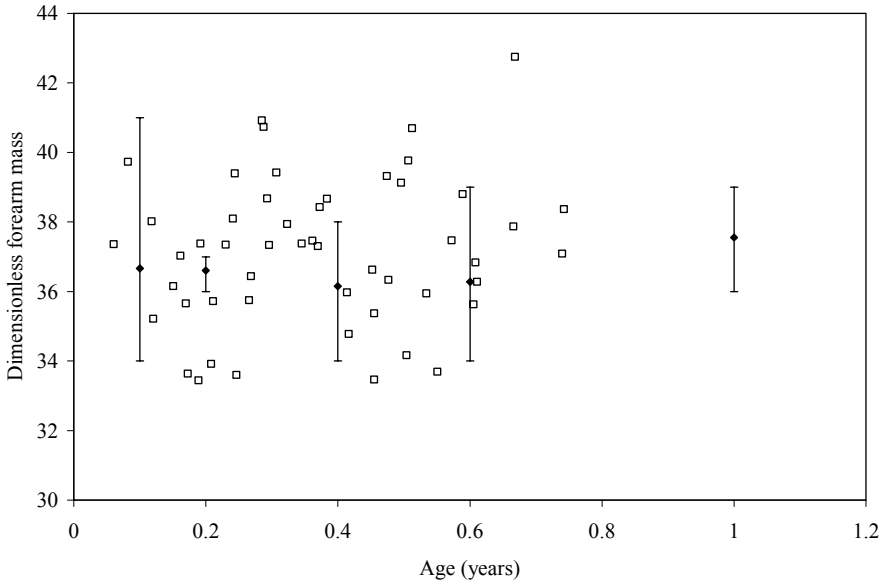


Figure 2.27. Comparison of infant baboon forearm masses as a percentage of forelimb mass with those of infant Macaca (data from Turnquist and Wells, 1994). Infant baboon values are open squares, mean values of *Macaca* at each age are closed diamonds, bars represent the range for infant *Macaca* at each age.

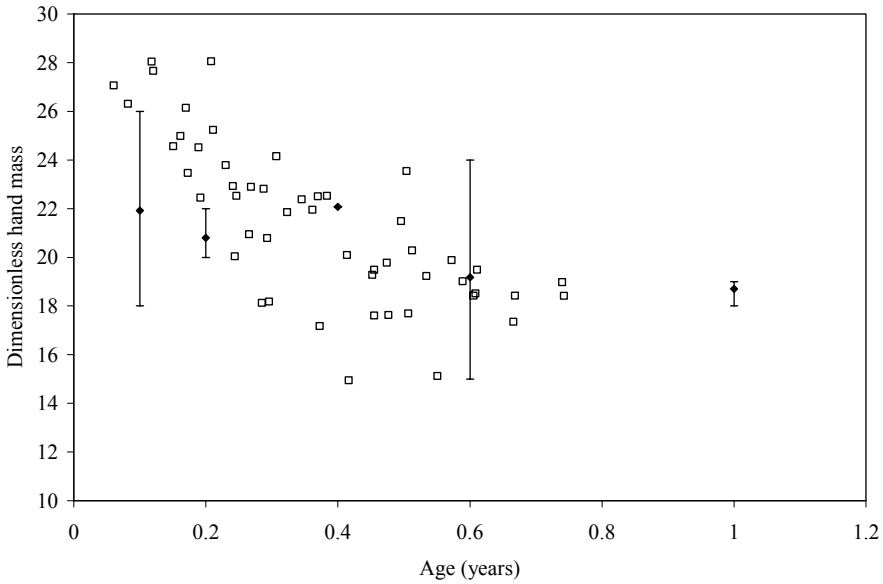


Figure 2.28. Comparison of infant baboon hand masses as a percentage of forelimb mass with those of infant Macaca (data from Turnquist and Wells, 1994). Infant baboon values are open squares, mean values of *Macaca* at each age are closed diamonds, bars represent the range for infant *Macaca* at each age.

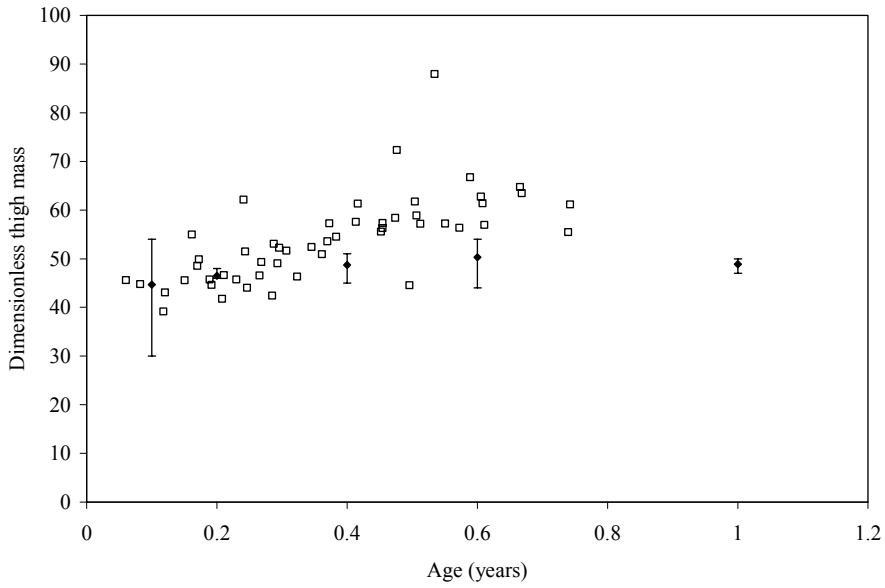


Figure 2.29. Comparison of infant baboon thigh masses as a percentage of hindlimb mass with those of infant Macaca (data from Turnquist and Wells, 1994). Infant baboon values are open squares, mean values of *Macaca* at each age are closed diamonds, bars represent the range for infant *Macaca* at each age.

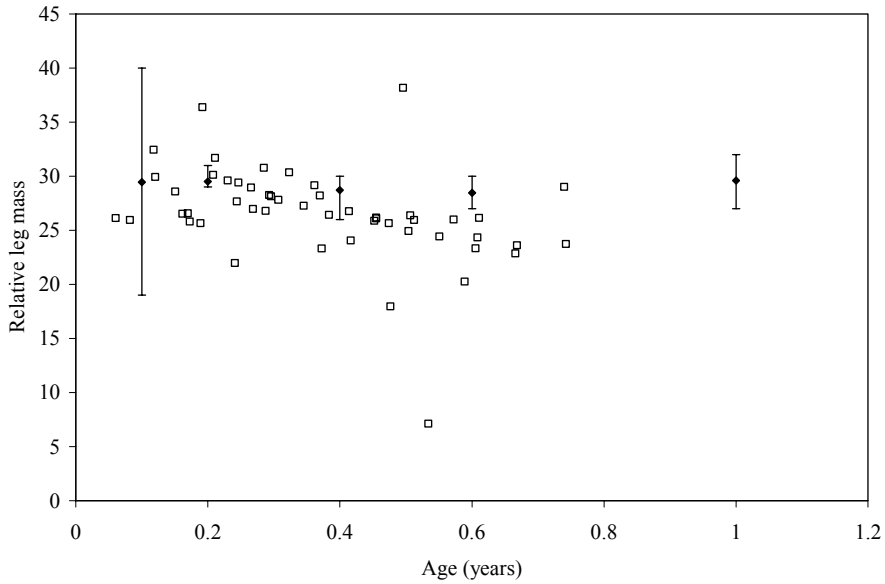


Figure 2.30. Comparison of infant baboon leg masses as a percentage of hindlimb mass with those of infant Macaca (data from Turnquist and Wells, 1994). Infant baboon values are open squares, mean values of *Macaca* at each age are closed diamonds, bars represent the range for infant *Macaca* at each age.

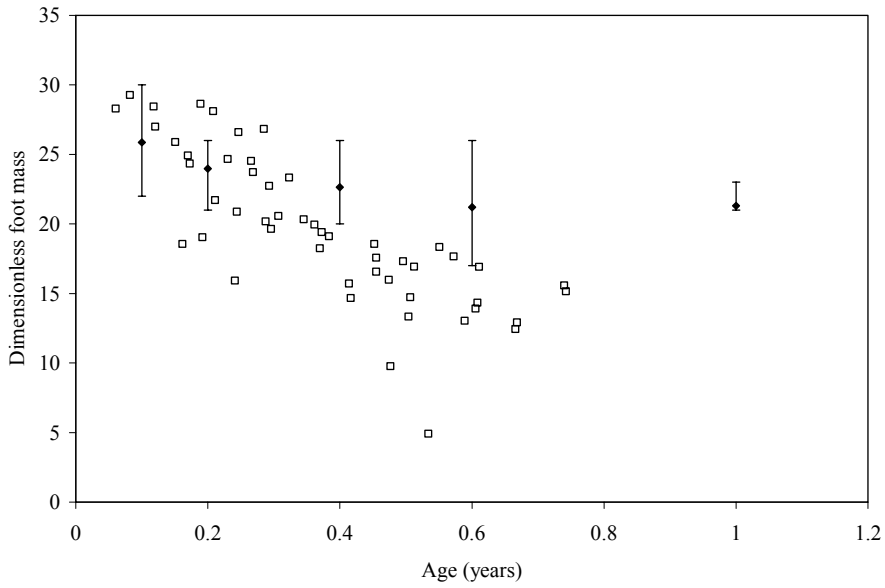


Figure 2.31. Comparison of infant baboon foot masses as a percentage of hindlimb mass with those of infant Macaca (data from Turnquist and Wells, 1994). Infant baboon values are open squares, mean values of *Macaca* at each age are closed diamonds, bars represent the range for infant *Macaca* at each age.

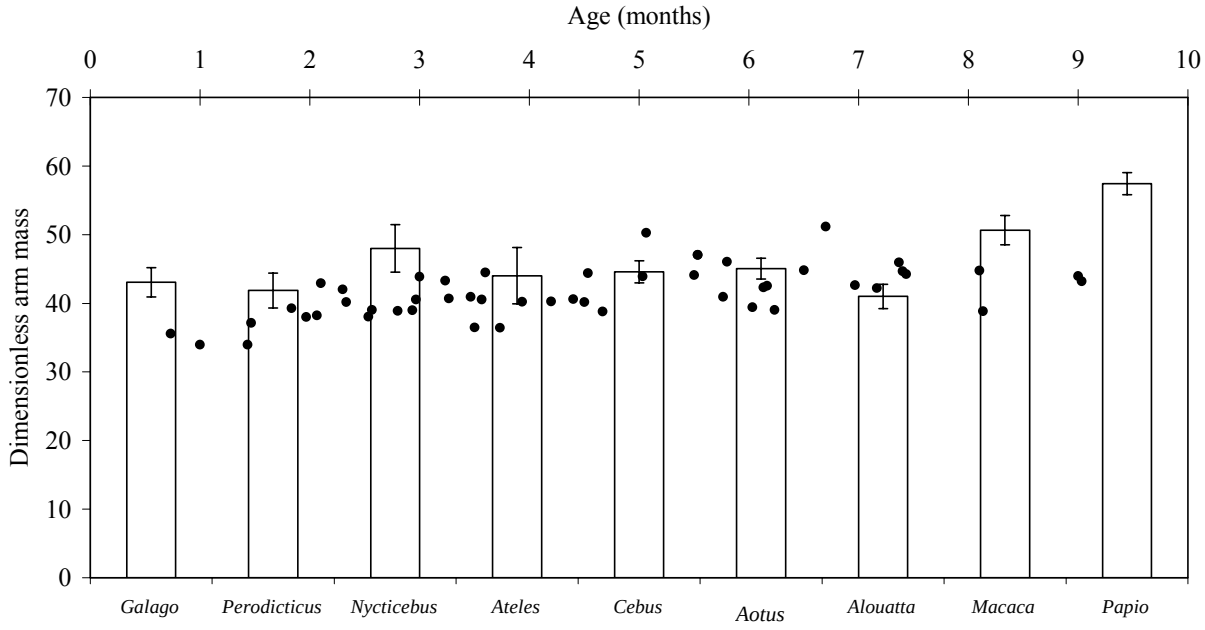


Figure 2.32. Comparison of infant baboon arm masses as a percentage of forelimb mass with those of adult primate taxa from Grand (1977) and Raichlen (2004). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

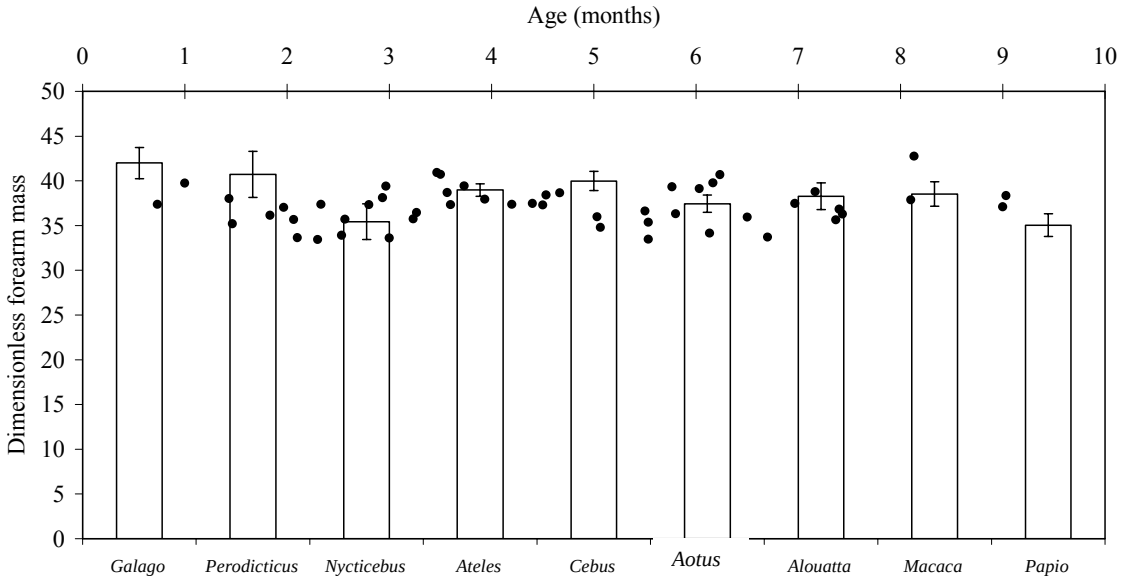


Figure 2.33. Comparison of infant baboon forearm masses as a percentage of forelimb mass with those of adult primate taxa from Grand (1977) and Raichlen (2004). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

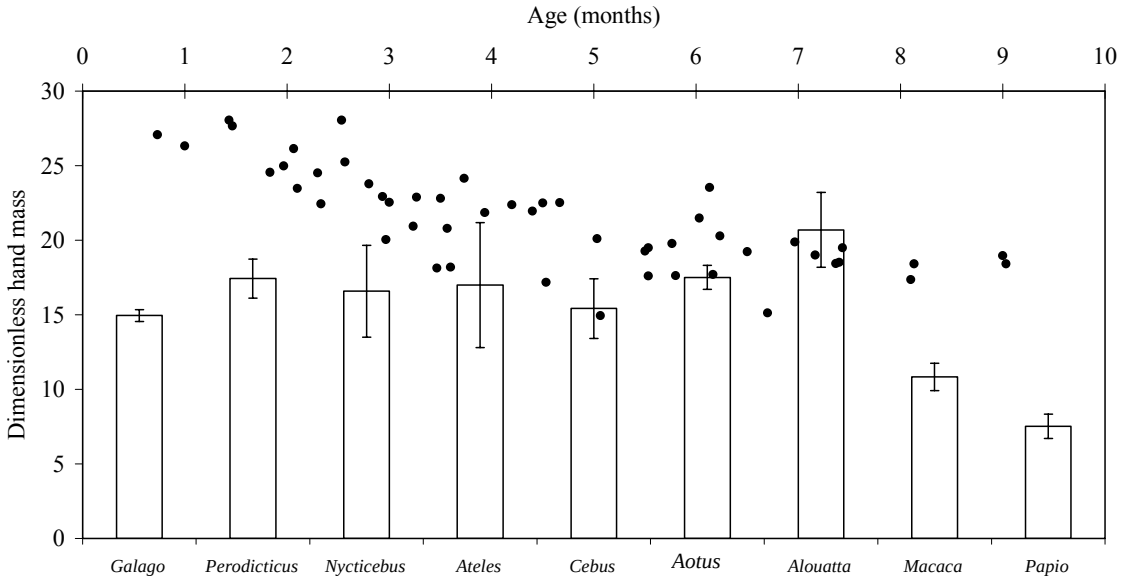


Figure 2.34. Comparison of infant baboon hand masses as a percentage of forelimb mass with those of adult primate taxa from Grand (1977) and Raichlen (2004). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

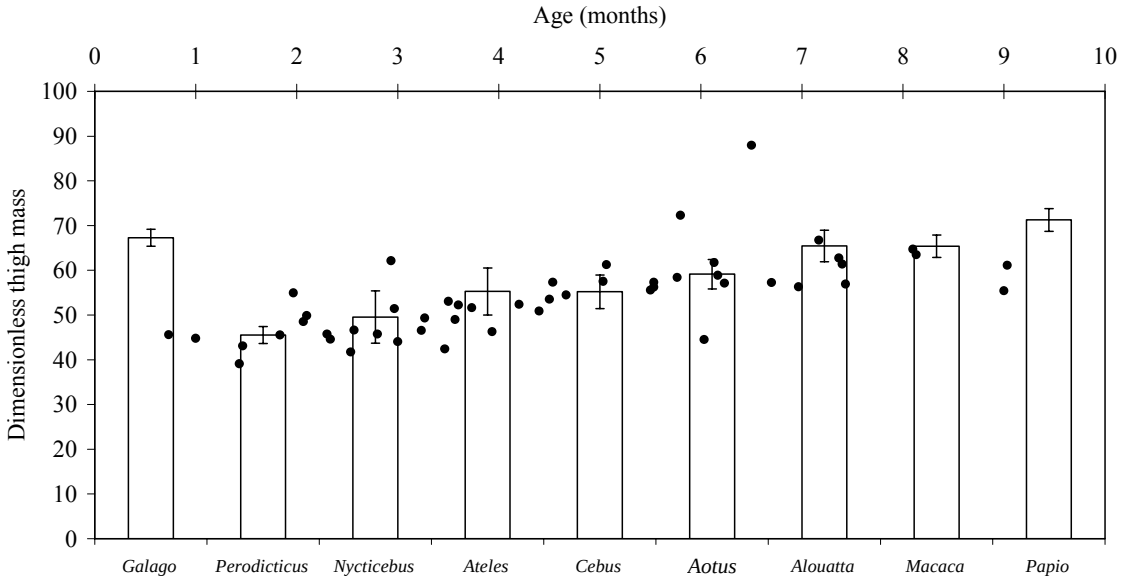


Figure 2.35. Comparison of infant baboon thigh masses as a percentage of hindlimb mass with those of adult primate taxa from Grand (1977) and Raichlen (2004). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

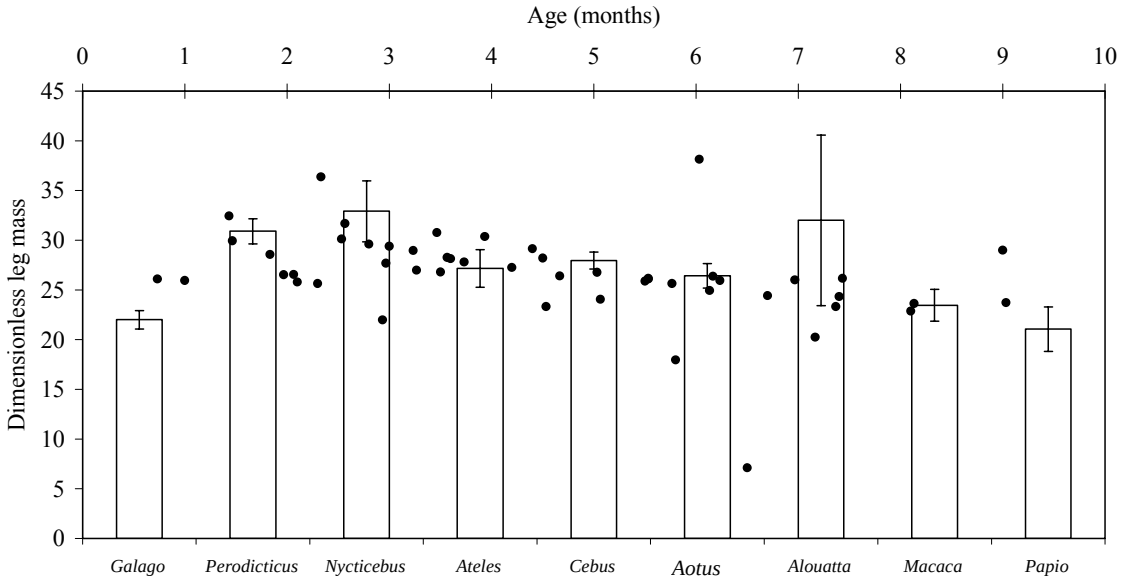


Figure 2.36. Comparison of infant baboon leg masses as a percentage of hindlimb mass with those of adult primate taxa from Grand (1977) and Raichlen (2004). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

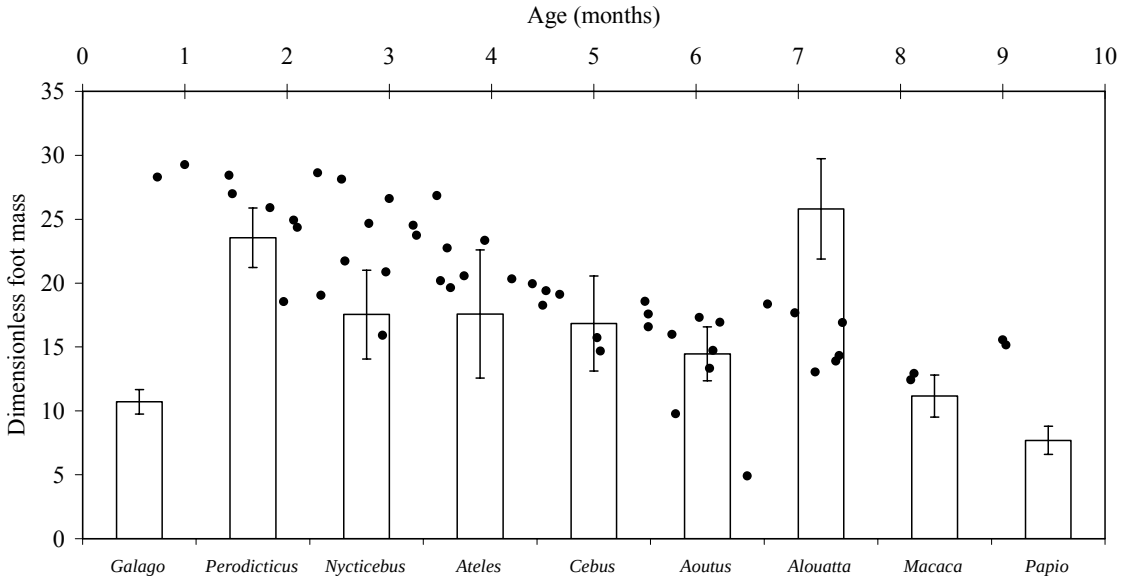


Figure 2.37. Comparison of infant baboon foot masses as *Aotus* ntage of hindlimb mass with those of adult primate taxa from Grand (1977) and Raichlen (2004). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

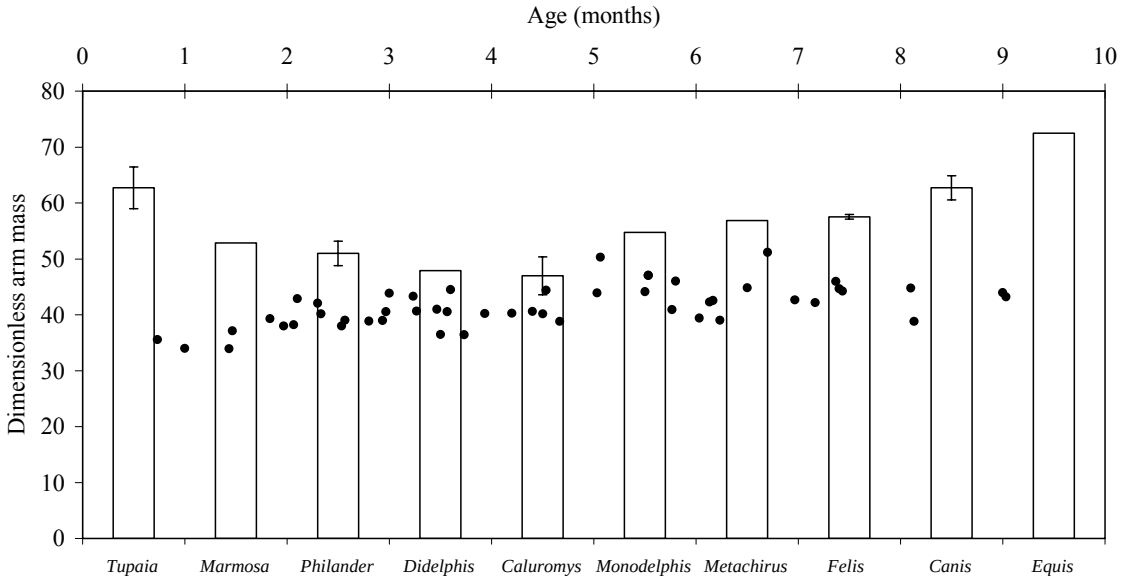


Figure 2.38. Comparison of infant baboon arm masses as a percentage of forelimb mass with those of adult non-primate taxa from Grand (1977; *Tupaia, Felis,* and *Canis*), Grand (1983; Didelphids), and Sprigings and Leach (1986; *Equis*). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

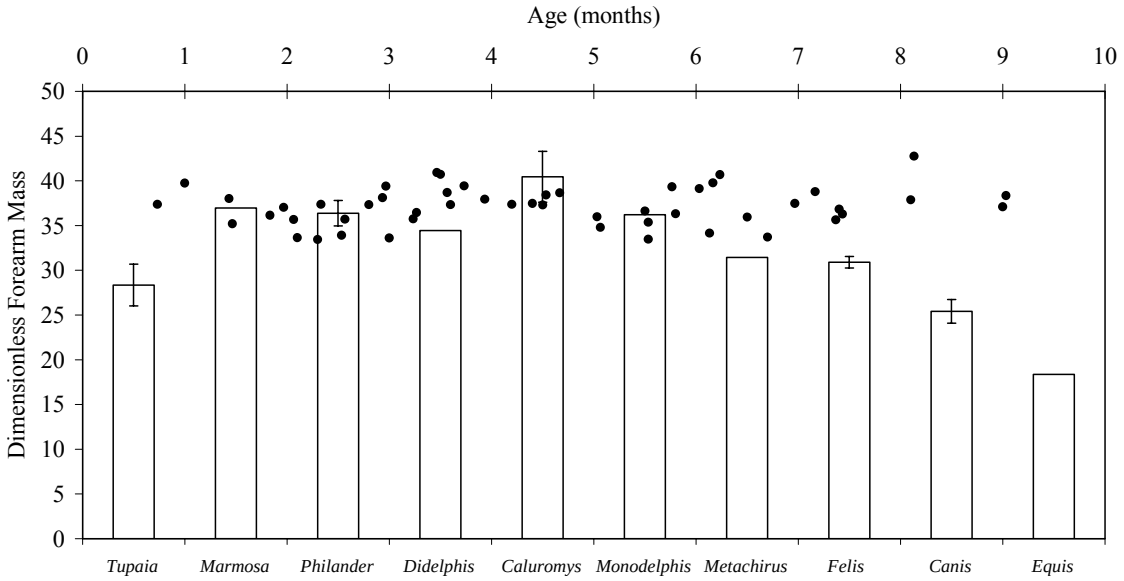


Figure 2.39. Comparison of infant baboon forearm masses as a percentage of forelimb mass with those of adult non-primate taxa from Grand (1977; *Tupaia, Felis,* and *Canis*), Grand (1983; Didelphids), and Sprigings and Leach (1986; *Equis*). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

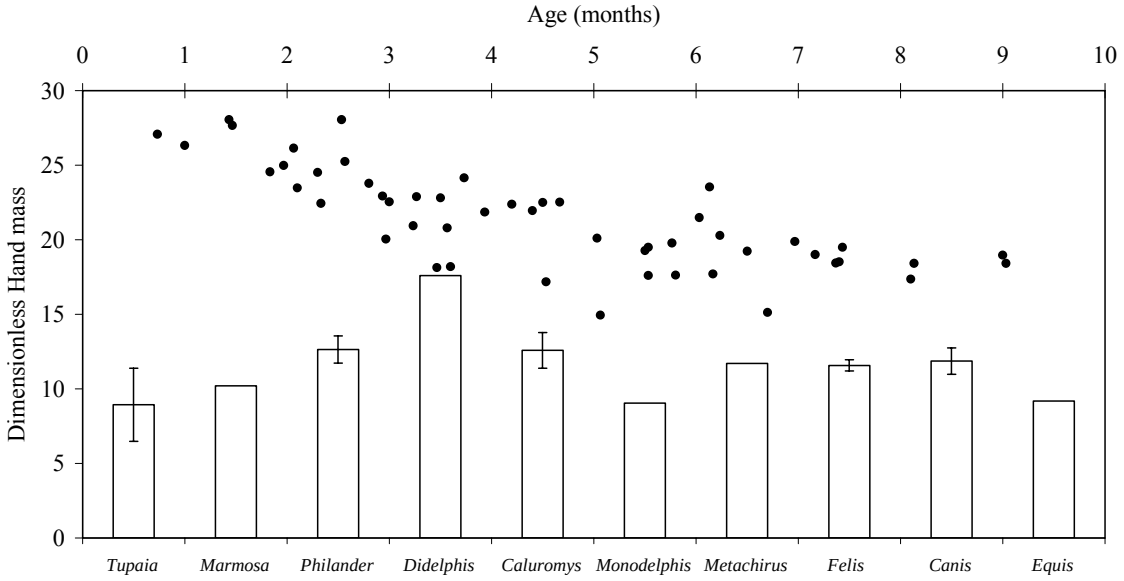


Figure 2.40. Comparison of infant baboon hand masses as a percentage of forelimb mass with those of adult non-primate taxa from Grand (1977; *Tupaia, Felis,* and *Canis*), Grand (1983; Didelphids), and Sprigings and Leach (1986; *Equis*). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

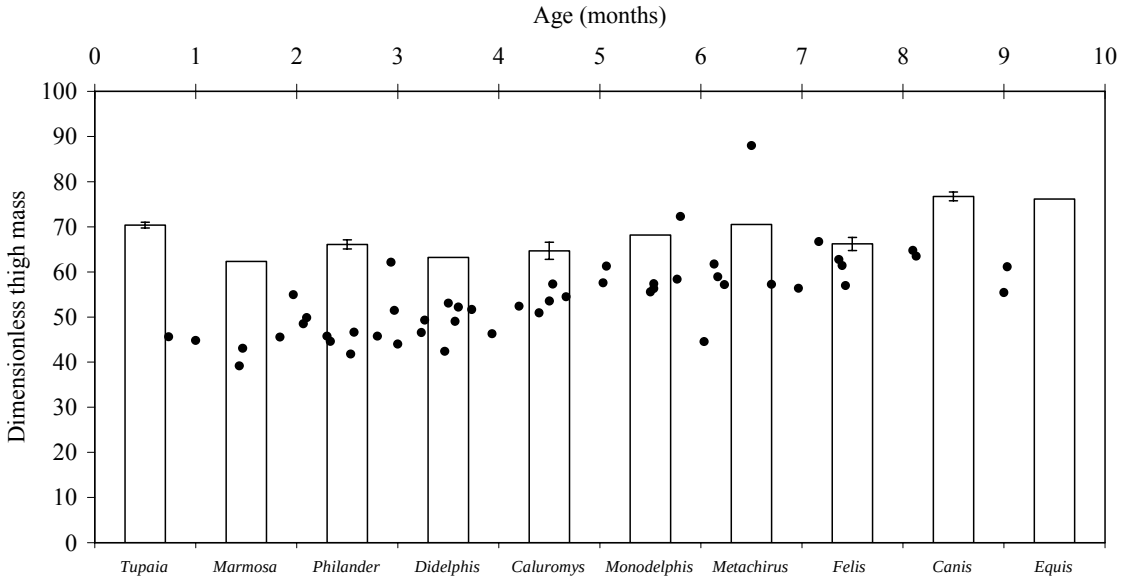


Figure 2.41. Comparison of infant baboon thigh masses as a percentage of hindlimb mass with those of adult non-primate taxa from Grand (1977; *Tupaia, Felis,* and *Canis*), Grand (1983; Didelphids), and Sprigings and Leach (1986; *Equis*). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

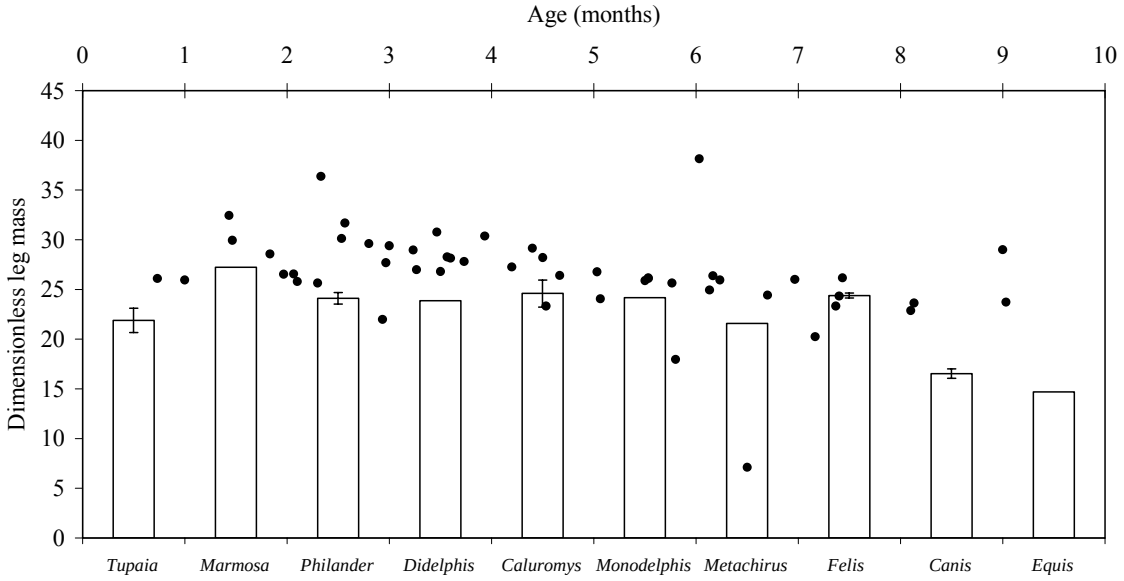


Figure 2.42. Comparison of infant baboon leg masses as a percentage of hindlimb mass with those of adult non-primate taxa from Grand (1977; *Tupaia, Felis,* and *Canis*), Grand (1983; Didelphids), and Sprigings and Leach (1986; *Equis*). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

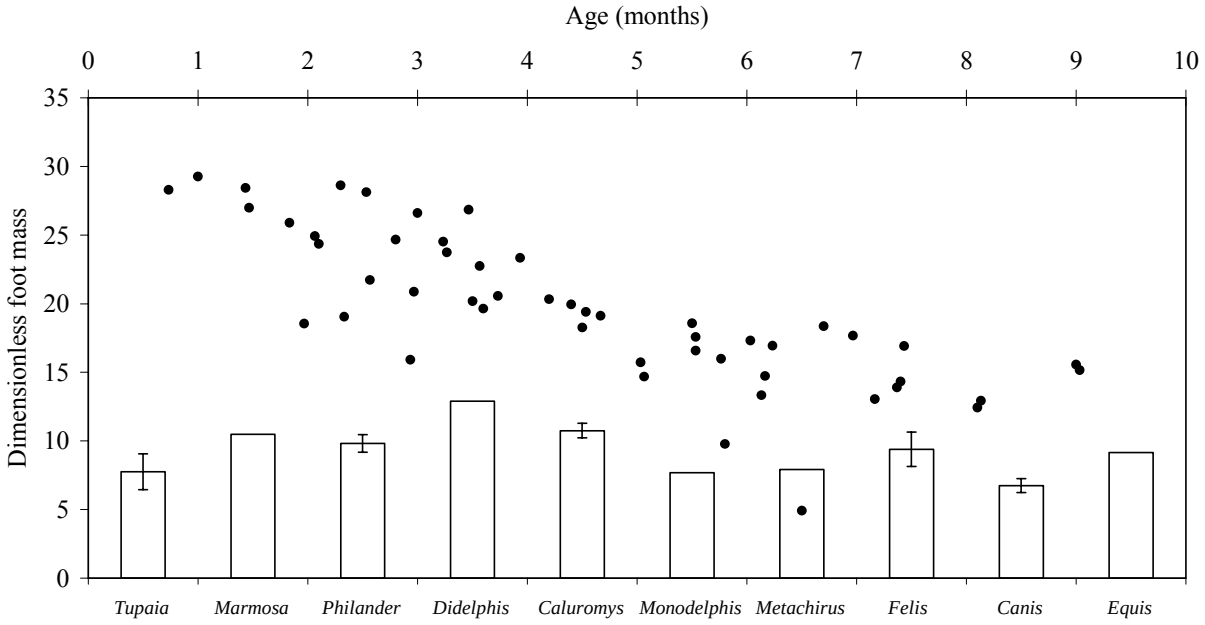


Figure 2.43. Comparison of infant baboon foot masses as a percentage of hindlimb mass with those of adult non-primate taxa from Grand (1977; *Tupaia, Felis,* and *Canis*), Grand (1983; Didelphids), and Sprigings and Leach (1986; *Equis*). Each column represents a mean for each primate taxon and the bars represent the 95% confidence limits of the mean.

CHAPTER 3

A Simple Model of Locomotion to Predict the Effects of Limb Mass Distribution on Quadrupedal Kinematics

INTRODUCTION

Primate quadrupeds use relatively long strides and low stride frequencies at a given velocity compared to non-primate quadrupedal mammals (Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1990). Because long strides and low stride frequencies reduce branch oscillations, these locomotor characteristics have been linked to others, such as large limb angular excursions and long contact times, as being adaptive for safe travel in a small branch arboreal environment, (Demes et al., 1990; Schmitt, 1998; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002; Cartmill et al., 2002; Schmitt, 2003). The small branch environment is thought to have been an important niche during early primate evolution (Cartmill, 1972, 1974, 1992). The small branch niche hypothesis for the evolution of primate quadrupedalism does not, however, fully account for the continued use of these unique kinematics when individuals are not walking in a small branch niche (including primates who are dedicated terrestrial quadrupeds).

A biomechanical model linking morphology to primate kinematics will undoubtedly further enhance our understanding of the evolution of primate quadrupedalism. In an attempt to develop such a model, Reynolds (1987) suggested that

the long strides of primate quadrupeds are related to their relatively long limbs. Long strides lead to low stride frequencies at a given velocity because velocity is the product of stride length and stride frequency. Although this hypothesis has intuitive appeal, any biomechanical explanation for the evolution of long strides and low stride frequencies in primates must also hold true for non-primates in general.

Several authors have postulated a relationship between long limbs and long strides among mammals in general (Schmidt-Nielson, 1984; Fancy and White, 1987; Reynolds, 1987; Janis and Wilhelm, 1993). Heglund and Taylor (1974, 1988) provided some empirical support for this idea. They showed that stride lengths increase with increasing body mass (and therefore limb length) at the trot-gallop transition velocity (Heglund and Taylor, 1974, 1988). This transition is considered to be a physiologically equivalent velocity, implying two animals of different body size can be compared directly at this velocity. The long limb hypothesis was not supported, however, when animals of similar size, yet with different limb lengths were examined. Williams (1983) and Williams et al. (2002) showed that the relatively short legged mink and otter have strides equal to or longer than those of similarly sized, and longer legged, quadrupeds at a given velocity.

Alexander and Jayes (1983) introduced a new method to compare the kinematics of animals of different body masses over a wide range of velocities. The dynamic similarity hypothesis proposed by Alexander and Jayes (1983) relies on the importance of gravitational and inertial forces in governing locomotor dynamics (see also Hof, 1996). If two animals are geometrically similar in body size, then their locomotion is considered to be dynamically similar if they have equivalent size-adjusted locomotor kinematics at

equivalent size adjusted velocities (Alexander and Jayes, 1983). The size-adjusted velocity suggested by Alexander and Jayes (1983) is the Froude number (v^2/gh; where v is velocity, g is gravitational acceleration, and h is a characteristic length variable). The Froude number is proportional to the ratio of kinetic ($1/2mv^2$) and potential energy (mgh), which implies that animals walking at equal Froude numbers have equal ratios of kinetic and potential energy (Alexander and Jayes, 1983).

This technique allows for a more complete examination of the effects of limb length on stride length and stride frequency in mammalian locomotion. Although Alexander and Jayes (1983) suggested that mammalian quadrupeds generally walk with dynamic similarity, they found that dimensionless stride lengths (stride length/limb length) were not dynamically similar across all groups of mammals at the same Froude numbers (Alexander and Jayes, 1983; Alexander and Maloiy, 1984). For example, primates walk with longer dimensionless strides at a given Froude number compared to non-primate quadrupeds (Alexander and Maloiy, 1984). Reynolds (1987) suggested that primates' long strides are due, in part, to their relatively long limbs compared to other quadrupedal mammals. The results of Alexander and Maloiy (1984) show that this is not the case. Since dimensionless stride length is calculated as stride length divided by limb length, relatively long limbs should create shorter dimensionless stride lengths in primates. Because differences in stride length remain after limb length has been taken into account, limb length alone cannot explain differences in stride lengths among quadrupeds.

The failure of the dynamic similarity hypothesis to explain variation in stride lengths among mammals may be rooted in the concept of geometric similarity. Although

mammals may exhibit geometric similarity in limb lengths, their limb shapes may not be geometrically similar. Limb mass distribution may be related to functions which do not necessarily scale with body mass in a predictable way (e.g. manual and pedal grasping abilities; see Chapter 2). As described in Chapter 2, increasingly distal limb mass concentrations increase the limb's natural pendular period of oscillation (NPP; see also Myers and Steudel, 1997), implying two quadrupeds with equal limb lengths can have different limb NPPs. Since the NPP is the time it takes the limb to swing through a single complete pendular oscillation, any increases in NPP should increase an individual's swing phase duration and therefore increase that individual's stride duration (see Holt et al., 1991; Myers and Steudel, 1997). Large NPPs should therefore lead to low stride frequencies because stride frequency is the reciprocal of stride duration. Finally, low stride frequencies are associated with relatively long strides at a given velocity.

In experimental studies where an individual's limb mass distribution is altered by adding mass to distal elements (increasing the limb's NPP), swing durations and stride durations increase significantly (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel 1990; Mattes et al., 2000). These studies suggest that limb mass distribution may play an important role in determining the spatio-temporal characteristics of an individual's stride and should therefore be included in the discussion of kinematic differences among animals that remain after correcting for body size.

This study examines the role of limb mass distribution in determining a quadruped's stride frequency and stride length from three perspectives. In this chapter a model is presented that predicts the effects of limb mass distribution on kinematics using very simple locomotor principles. In Chapter 4, locomotor kinematics in a sample of

infant baboons (*Papio cynocephalus*) are analyzed as their limb mass distributions change during ontogeny (see Chapter 2). This type of study provides an ontogenetic "natural experiment" to determine how strongly limb shape influences locomotor kinematics. The kinematics of the infant baboons are also compared to the kinematics of adult primates and non-primates. The hypothesis that limb mass distribution influences kinematics will be supported if all three lines of evidence provide similar results.

MODEL OF LOCOMOTION

The model presented in this study is based on one developed by Reynolds (1987) to explain the determinants of stride length and depends only on the mass distribution of the limb and its length to describe the fundamental locomotor kinematics of that individual at a given velocity. Models of varying complexity have been used to explore mammalian locomotor kinematics (see for example McMahon, 1975; Alexander, 1976; Mochon and McMahon, 1980,1981; McGreer, 1990a,b; Minetti and Saibene, 1992; Anderson and Pandy, 2001; Alexander, 2003). Alexander (2003) discusses the advantages of very simple models for describing human locomotion. If a model has relatively few inputs, then its results help reduce the complexity of locomotion to simple rules (Alexander, 2003). Therefore, an attempt here was made to create an exceedingly simple, yet accurate, model with the fewest possible inputs. As with any model, several simplifying assumptions must be made. The validity of these assumptions and support for the model's prediction will be discussed below.

Reynolds (1987) described the contributions of stance phase kinematics and swing phase kinematics to total stride length by modeling the hindlimb as a single rigid

element (see Fig. 3.1). The distance traveled during stance phase (step length; L_1) is a function of limb angular excursion (θ) and limb length (h) after Reynolds (1987):

$$L_1 = 2h\sin(\frac{\theta}{2}) \quad (3.1)$$

If the animal is moving at a constant velocity (v), then this distance can also be calculated with knowledge of the duration of stance phase (t_c; see also Cavagna et al., 1977; Hoyt et al., 2000):

$$L_1 = vt_c \quad (3.2)$$

The distance traveled during swing phase (L_2) can be calculated with knowledge of velocity and the duration of swing phase (t_s):

$$L_2 = vt_s \quad (3.3)$$

Stride length and stride frequency are easily predicted as the sum of L_1 and L_2 and as the reciprocal of the sum of t_c and t_s respectively. By making simplifying assumptions about these parameters, Reynold's (1987) model may be expanded to predict locomotor kinematics at a given velocity based simply on a given subject's limb length and the distribution of mass along that length. I will first describe the assumptions and how they relate to the model. The validity of these assumptions will be described in a later section (see **Model Assumptions** below).

First, it is assumed that step length (L_1) does not change with increasing velocity (see Kram and Taylor, 1990). If L_1 does not change with velocity, then from equation 3.2, it is evident that the following must be true:

$$t_c \propto v^{-1} \quad (3.4)$$

The second assumption is that swing duration (t_s) remains constant with increasing velocities and that the limb swings as a pure pendulum. This assumption has been used in other successful locomotor models (see McMahon, 1975; Mochon and McMahon, 1980, 1981). Therefore, swing duration will approximate half of the limb's NPP:

$$t_s = \frac{NPP}{2} \tag{3.5}$$

Finally it is assumed that animals change velocities using Hildebrand's (1966) definition of walks and runs. Hildebrand (1966) defined walks as any gait where hindlimb stance duration is greater than 50% of total stride duration, and runs as any gait where hindlimb stance duration is less than 50% of total stride duration. So, at the transition between walking and running, hindlimb stance duration would be 50% of stride duration and equal to hindlimb swing duration.

The first step in determining an animal's locomotor kinematics using this model is to calculate the hindlimb's natural pendular period (NPP). The NPP is based on the limb's mass distribution (see Myers and Steudel, 1997; Raichlen, 2004; Chapter 2) and is equal to the duration of one complete oscillation of the limb as it swings as a pure pendulum (see Chapter 2).

$$NPP = \sqrt{\frac{I}{mgCM}} \tag{3.6}$$

where I is the limb's mass moment of inertia about a transverse axis through the proximal limb joint, m is the limb's mass, CM is the distance of the limb's center of mass from the proximal end, and g is gravitational acceleration (9.8 ms^{-2}).

Researchers have found that the change in t_c with velocity is best described by a power function (Demes et al., 1990; Hoyt et al., 2000). Given the assumption of equation 3.4, this function can be written as:

$$t_c = av^{-1} \tag{3.7}$$

The factor a is calculated with the knowledge that, at the walk-run transition, when duty factor equals 50, swing duration and stance duration are equal:

$$t_c = t_s = av_{w/r}^{-1} \tag{3.8}$$

where $v_{w/r}$ is velocity at the walk run transition. Rearranging equation 3.8 expresses factor a as a function of t_s and v:

$$a = \frac{t_s}{v_{w/r}^{-1}} \tag{3.9}$$

The velocity at the walk-run transition is estimated from the dynamic similarity model developed by Alexander and Jayes (1983). They found that quadrupeds generally transition from a walk to a run at similar dimensionless velocities (Froude number ≈ 0.4; Alexander and Jayes, 1983). The equation for Froude number (F) is:

$$F = \frac{v^2}{gh} \tag{3.10}$$

Rearranging equation 3.10 gives v as a function of F, h, and g:

$$v = \sqrt{Fgh} \tag{3.11}$$

So factor a may be calculated by substituting equation 3.11 with a Froude number of .4 into equation 3.9:

$$a = \frac{t_s}{\left(\sqrt{.4gh}\right)^{-1}} \tag{3.12}$$

The choice of velocities for calculation of model parameters is arbitrary and for this model, parameters will be calculated at a variety of Froude numbers. At a given Froude number, velocity is calculated using equation 3.11, stance duration is calculated using equation 3.7, step length is calculated using equation 3.2, swing length is calculated using equation 3.3, t_s is equal to half the limb's NPP (eq. 3.5), and hindlimb excursion during stance phase is calculated using equation 3.1. Finally stride length (SL) and stride frequency (SF) are simply:

$$SL = L_1 + L_2 \tag{3.13}$$

$$SF = \frac{1}{t_c + t_s} \tag{3.14}$$

To determine whether the model follows the predictions of dynamic similarity, dimensionless stride lengths (dSL) and frequencies (dSF) were calculated after Alexander and Jayes (1983) and Hof (1996; see also Zjilstra, 1996; Aerts et al., 2000):

$$dSF = \frac{SF}{\sqrt{\frac{h}{g}}} \tag{3.15}$$

$$dSL = \frac{SL}{h} \tag{3.16}$$

Model assumptions

The assumptions of the model have a large impact on the predicted stride lengths and frequencies. Therefore, it is essential to examine if, and how often these assumptions are violated.

First, the model assumes that stance duration (t_c) changes in proportion to velocity$^{-1.0}$. Demes et al. (1990) reported regression equations for the relationship between stance duration and velocity in two strepsirhine primates (*Loris tardigradus* and *Nycticebus coucang*). They found that in both of these species, the slopes of the log transformed regression lines relating limb stance duration and velocity (*Loris*: -0.98; *Nycticebus*: -0.92) were within 2 standard errors of -1.0 (see Demes et al., 1990; their Table 5). Vilensky et al. (1988) reported that vervet monkeys decrease stance durations in proportion to velocity$^{-0.9}$, and this exponent is within 2 standard deviations of -1. Hoyt et al. (2000), however, found that time of contact decreased with velocity with a slope that is significantly shallower than -1.0 in 4 quadrupedal mammals (squirrel, dog, pony, and horse).

Step length and limb angular excursion can be used to provide further information on the relationship between stance duration and velocity for more taxa who do not have this relationship explicitly reported. If stance duration decreases with velocity$^{-1.0}$, then step length and limb angular excursion should be independent of velocity (see eqs. 3.1 & 3.2). The relationship between step length and velocity appears to be quite variable in terrestrial locomotion. Several researchers have found that step length does not change with velocity in a significant way (vervet monkeys: Vilensky et al., 1988; birds: quadrupedal mammals: Kram and Taylor, 1990; Roberts et al., 1998; Abourachid, 2001;

male patas monkey, vervet monkeys: Polk, 2001) while others found changes in step length with velocity (dogs: Blaszczyk and Dobrzecka, 1989; bonobos: Aerts et al., 2000; mammals and birds: Hoyt et al., 2000; female patas monkey, baboons: Polk, 2001).

Hindlimb angular excursion also shows a highly variable relationship with velocity in quadrupeds and bipeds. In many taxa, hindlimb angular excursion is not correlated with velocity (vervets: Vilensky and Gankiewiscz, 1990; quails: Reilly, 2000; monkeys: Polk, 2002; brown lemur and chimpanzee: Reynolds, 1987) while others have shown that angular excursion is correlated with velocity (monkeys: Vilensky et al., 1988; Polk, 2002; spider monkey and chimpanzee: Reynolds, 1987).

The model also assumes that swing duration is equal to half the limb's NPP. There have been suggestions, though, that limb motion during swing phase is not passive, but is driven by muscular action (see Jungers and Stern, 1983; Whitessely et al., 2000). Whitesseley et al. (2000) provides a convincing case for the non-passive nature of swing phase based on the inability of pure pendular motion to completely predict the kinematics and kinetics of human swing phase (see also Selles et al., 2001). Additionally, muscles acting on the shoulder and hip are active during swing phase in both humans and quadrupeds, although this activity is concentrated mostly at the beginning and the end of swing phase (Basmajian, 1978; English, 1978a,b; Goslow et al., 1981; Larson and Stern, 1989; Whitehead and Larson, 1994; but see Larson and Stern, 2004 for evidence that some strepsirhines have a greater amount of swing phase muscle activity).

Although the limbs of terrestrial mammals do not appear to swing without muscular action, there is strong evidence that the swing periods of humans and quadrupeds approximate their limb NPPs (Mochon and McMahon, 1980; Hildebrand,

1985; Turvey et al., 1988; Holt et al., 1990). Additionally, increasing limb NPPs by loading distal limb elements in both humans and quadrupeds significantly increases stride durations and swing durations (Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel 1990; Mattes et al., 2000). Therefore, despite the evidence that swing phase during walking may not be achieved by a purely passive pendular mechanism, limb NPPs may be used as qualitative predictor of swing phase mechanics. That is, larger NPPs should be associated with longer swing phase durations, although the actual swing times may not be equivalent to those predicted from limb NPPs.

Finally, the model assumes that swing duration remains constant as velocity increases. Swing duration appears to be either independent of velocity (macaques, Vilensky, 1983; humans, cats, Vilensky and Gehlson, 1984; vervets, Vilensky and Gankiewicz, 1986; Vilensky and Patrick, 1985; Vilensky et al., 1988; birds: Arbourachid, 2001; Reilly, 2000;) or decreases slightly with velocity in quadrupeds (humans, cats, Vilensky and Gehlson, 1984; squirrel monkey, Vilensky and Patrick, 1985; loris, Demes et al., 1990).

It is clear from the discussion above that taxa do not always conform to the assumptions of the locomotor model yet the source of this variability is currently unknown. The locomotor model links several spatio-temporal kinematic variables and therefore may be able to examine the effects of variability in a single assumption on other kinematic variables. Therefore, in addition to making kinematic predictions based on the model using the assumptions described above, the effects of violating these assumptions will be examined in detail.

RESULTS

Model Accuracy

The most complete way to test the accuracy of this model is to examine how well it predicts a known animal's kinematics given its known limb inertial properties. These data are not readily available in the literature, but a test was performed using kinematic data and inertial properties for an adult male baboon and an adult male patas monkey from Polk (2001; unpublished data). The predicted dimensionless stride lengths are remarkably similar to the actual dimensionless stride lengths used by these two subjects at a given Froude number (Figs. 3.2 & 3.3).

A second test was performed to determine how well the model predicts known relationships between body mass and kinematics at the trot-gallop transition velocity. Heglund and Taylor (1974) have shown that stride length increases with increasing body mass ($SL = 4.5M^{0.38}$), and stride frequency decreases with increasing body mass ($SF = .35M^{-0.14}$) at the trot-gallop transition.

To test how well the model predicts these known relationships, body masses and limb lengths were taken from Hoyt et al. (2000; see Table 3.1) for six mammalian quadrupeds. Limb NPPs were determined by scaling the limb NPP of a canid from Myers and Steudel (1997) to the limb lengths of the individuals from Hoyt et al. (2000) assuming that limb NPP scales with geometric similarity (see Myers and Steudel, 1997). This scaling was accomplished by calculating the dimensionless hindlimb NPP from dog #1 in Myers and Steudel (1997). If two animals have geometrically similar limb NPPs, then their dimensionless limb NPPs should be equivalent. The dimensionless limb NPP

(dNPP) for dog #1 from Myers and Steudel (1997) was calculated using the methods of Hof (1996):

$$dNPP_{dog\#1} = \frac{NPP_{dog\#1}}{\sqrt{\frac{h_{dog\#1}}{g}}} \tag{3.17}$$

Limb NPPs for the individuals from Hoyt et al. (2000) may then be calculated as:

$$NPP_i = dNPP_{dog\#1} \times \sqrt{\frac{h_i}{g}} \tag{3.18}$$

where NPP_i is the hindlimb NPP for each individual (i) from Hoyt et al. (2000) and h_i is the hindlimb length for each of those individuals. Finally, trot-gallop transition velocity was calculated according to the relationship between trot-gallop transition velocity (V_{tg}) and body mass from McMahon (1975):

$$V_{tg}=(5.5M^{.24})*3.6. \tag{3.19}$$

The model predicts that stride frequency at the trot-gallop transition decreases with increasing body mass ($SF=2.26BM^{-0.13}$; Fig. 3.4) and stride length at the trot gallop transition increases with increasing body mass ($SL=.676BM^{0.37}$; Fig. 3.5). The scaling exponents agree very well with the empirical results of Heglund and Taylor (1974), again supporting the accuracy of model predictions across a broad range of body sizes. Additionally, these results suggest that the scaling of stride frequency and stride length with body mass may simply be due to geometric scaling of limb inertial properties. The intercept values for the predicted equations and the empirical equations from Heglund and Taylor (1974) do, however differ. These differences may be the result of using

scaled limb inertial properties, rather than each individual's inertial properties, as model inputs.

Effects of body mass on modeled parameters

Two individuals from the Hoyt et al. (2000) sample had their stride lengths and stride frequencies predicted over a wide range of velocities to test for dynamic similarity (Figs. 3.6 & 3.7). The individuals walked with dynamically similar stride lengths and stride frequencies at a given dimensionless velocity. This is a very important result as it suggests that dynamic similarity is valid if animals are geometrically similar in both their limb lengths and their limb inertial properties.

The model suggests that in geometrically similar quadrupeds, limb angular excursion should not change with increasing body mass (Table 3.1). McMahon (1975) proposed that angular excursion should decrease with increasing body mass based on his elastic similarity hypothesis and provided some data in support of this idea. Reynolds (1987) showed, however, that primates deviate from McMahon's (1975) predictions. In fact, Reynold's (1987) primates all had very similar limb angular excursions despite an 18kg difference in body mass. Additionally, contrary to McMahon's (1975) prediction, the smallest primate in Reynold's (1987) study (*Lemur fulvus*, 2.0 kg) had a slightly smaller hindlimb excursion compared to the larger primates (although it was still similar to those of the larger bodied individuals).

Larson et al. (2001) showed that not only do primates in general have increased hindlimb angular excursions compared to other mammals, but that there is great variation in hindlimb angular excursion within non-primate terrestrial mammals in general.

Although the angles in Larson et al's (2001) analysis were calculated at preferred velocities rather than trot-gallop transition velocities, the scatter about the trend lines relating hindlimb angular excursion and body mass is quite striking (see Larson et al., 2001; their Figure 2). Within taxonomic groups (e.g. ungulates, carnivores, etc.), the points do not appear to follow a strong trend. The least squares means (LSmean) calculated from ANOCOVA for hindlimb angles in all taxa with body mass as the covariate do not differ greatly from the means (see Larson et al., 2001). The lack of difference between the mean and the LSmean for each taxonomic group indicate that body size has only a minimal effect on hindlimb angular excursion. These data indicate that there is some variability in limb angular excursion among mammals that is not explained by body mass alone contrary to McMahon (1975).

Effects of limb mass distribution on modeled parameters

One infant baboon had its locomotor kinematics modeled at two ages when its dimensionless inertial properties differed (Table 3.2). Hindlimb mass is more distally distributed at the younger age for this individual leading to a large dimensionless hindlimb NPP. Raw NPPs are, however, quite similar, suggesting similarity in swing durations. Therefore, the model will be used to predict the kinematics of this individual at two ages where swing phase durations are equal (because NPPs are equal), but limb lengths and body masses are not.

Table 3.3 gives the modeled kinematics at a given velocity for this infant baboon at both ages. When young, this individual used longer dimensionless stride lengths and lower dimensionless stride frequencies compared to its modeled kinematics at the older

age (Figs. 3.8 & 3.9). This relationship occurs despite the fact that its raw stride frequencies are higher and its raw stride lengths are shorter than when it is younger (Figs. 3.10 & 3.11). Therefore, the model predicts that relatively distal limb mass concentrations will lead to long dimensionless strides and low dimensionless stride frequencies.

Increases in dimensionless stride length are due to increases in dimensionless step length (dL_1) and increases in the dimensionless distance traveled during swing phase (dL_2; Table 3.3). It is important to note that the difference in step length is the result of longer dimensionless stance durations when the infant is young. This increased stance duration is a direct result of the increased swing duration at a given velocity. Stance duration must remain larger than swing duration during walking because, during walking gaits, the percentage of the stride that a limb is in stance duration (duty factor) is greater than 50. Any increase in swing duration must therefore be met by an increase in stance duration. These results suggest an important connection between swing and stance durations.

Effects of violating the model assumptions

The assumptions used to create the model are certainly violated with some frequency in mammalian taxa. Based on the evidence cited above, it is important to examine how violations of the model assumptions will influence locomotor variables. If stance duration does not decrease in direct proportion to velocity (factor a in equation 3.7 is not equal to -1.0), then the slope of the line relating dimensionless stride length and Froude number changes (Fig. 3.12). Dimensionless stride length increases at a higher

rate if factor a is greater than -1 and increases at a lower rate if factor a is less than -1. The slope of the line relating dimensionless stride frequency and Froude number also changes if factor a is not equal to -1. Dimensionless stride frequencies increase at a lower rate if factor a is greater than -1 and at a higher rate if factor a is less than -1 (Fig. 3.13).

If swing duration is not constant as velocity increases, the slope of the line relating dimensionless stride length and Froude number will change. When swing duration is not constant, it decreases with increasing velocity (*Loris* and *Nycticebus*, Demes et al., 1990; *Homo*, *Felis*, Vilensky and Gehlson, 1984; *Saimiri*, Vilensky and Patrick, 1985) and dimensionless stride lengths will increase at a lower rate, while dimensionless stride frequencies will increase at a higher rate with increasing dimensionless velocity (Figs. 3.14 & 3.15).

There is some evidence that non-primate mammalian quadrupeds may actually conform more to violations of these assumptions in their actual stride lengths and frequencies. In mammalian quadrupeds, the slopes of the regression lines relating raw stride length and body mass and raw stride frequency and body mass differ in mammalian quadrupeds in a consistent way (Strang and Steudel, 1990). Stride length increases at a higher rate, and stride frequency increases at a lower rate with increasing velocity in larger bodied mammals compared to smaller bodied mammals (Strang and Steudel, 1990).

Strang and Steudel's (1990) results may be explained by the predictions of the locomotor model when assumptions are violated. Specifically, as described above, the effects of varying the relationship between stance duration and velocity can impact the

rates of changes of stride frequency and stride length with increasing velocity. That is, if factor a in equation 3.7 is larger in a larger bodied individual compared to a smaller bodied individual, then its stride lengths would increase at a higher rate and its stride frequencies would increase at a lower rate with increasing velocity compared to the smaller bodied individual. Hoyt et al. (2000) showed that there was a trend, although not significant, in their four individual quadrupeds for factor a to increase with increasing body size. This relationship remains to be tested among a larger sample of taxa, but may explain the body size related differences in rates of increase in stride length and stride frequency among mammalian quadrupeds.

Discussion

The model predicts spatio-temporal kinematics (stride and step lengths, stride frequencies, stance and swing durations) of mammalian quadrupeds based simply on limb lengths and limb inertial properties. The accuracy of such a simple model in predicting these variables suggests that the relatively simple mechanism of pendular swinging of the limbs during their aerial phases plays an important role in determining kinematic variables. Additionally, the model highlights the inter-relatedness of spatio-temporal kinematics during quadrupedalism. For example, an alteration in the stance durations with changes in velocity may have large impacts on an individual's stride length and stride frequency.

The assumptions of the model do not apply to all empirical data, as reported above. It is still unclear why some individuals follow the assumptions, while others

violate them. Understanding this variability must be considered an important area of future research.

Based on the predictions made by the model for the effects of limb mass distribution on kinematics, several hypotheses may be developed for empirical studies examining individuals who differ in their limb mass distributions. Individuals with relatively more distal limb mass concentrations should have relatively long swing durations. These relatively long swing durations should lead to relatively long stance durations due to the need to maintain longer stance compared to swing durations during walking gaits. Combined, these relatively long swing and stance durations should lead to relatively long strides and long stride durations (low stride frequencies) in individuals with relatively distal limb mass concentrations. These hypotheses will be tested in Chapter 4 using the ontogenetic infant baboon sample.

TABLES

Table 3.1. Model parameters for test of accuracy of model predictions of kinematics over a wide range of body sizes.

Variable	Kangaroo Rat (*Dipodomys merriami*)	Squirrel (*Spermophilus tridecemlineatus*)	Spring Hare (*Pedetes capensis*)	Dog (*Canis familiarus*)	Pony (*Equis caballus*)	Horse (*Equis caballus*)
Body mass	0.03	0.21	3.00	25.80	141.00	450.00
Hindlimb Length	0.06	0.10	0.31	0.47	0.83	1.19
Predicted NPP	0.33	0.42	0.75	0.93	1.23	1.47
Velocity	0.67	1.05	1.99	3.33	5.01	6.62
limb length	0.06	0.10	0.31	0.47	0.83	1.19
NPP	0.33	0.42	0.75	0.93	1.23	1.47
stance duration	0.12	0.13	0.21	0.19	0.22	0.24
step length	0.08	0.13	0.41	0.63	1.10	1.59
swing length	0.11	0.22	0.75	1.55	3.07	4.87
stride length	0.19	0.35	1.16	2.18	4.17	6.46
stride frequency	3.55	2.97	1.71	1.53	1.20	1.03
hindlimb excursion	41.85	41.85	41.85	41.85	41.85	41.85

Mammalian body masses and limb lengths from Hoyt et al. (2000). See text for a description of how NPPs and model parameters were calculated.

Table 3.2. Inertial property variables used for predictions of the effects of limb mass distribution on locomotor kinematics

Age (months)	Body Mass (g)	Hindlimb Length (cm)	Hindlimb Mass (g)	Hindlimb CM (cm)	Hindlimb I (g cm^2)	Hindlimb NPP (s)	Dim NPP
6.97	2276.47	20.60	283.16	12.71	66455.46	0.86	5.95
7.43	2438.84	32.50	317.95	12.84	75520.61	0.86	4.74

Note: All inertial properties are raw values. NPP is given as a raw value and a dimensionless (dim) value.

Table 3.3. Predicted kinematics for infant baboon with different limb mass distributions.

Age 1 (6.97 months)

Froude	velocity	limb length	NPP	t_c	L_1	L_2	SL	SF	dSL	dSF	dL_1	dL_2	dt_c
0.10	0.45	0.21	0.86	0.86	0.39	0.19	0.58	0.78	2.81	0.11	1.87	0.94	5.93
0.20	0.64	0.21	0.86	0.61	0.39	0.27	0.66	0.96	3.20	0.14	1.87	1.33	4.19
0.30	0.78	0.21	0.86	0.50	0.39	0.33	0.72	1.08	3.50	0.16	1.87	1.62	3.42
0.40	0.90	0.21	0.86	0.43	0.39	0.39	0.77	1.16	3.75	0.17	1.87	1.88	2.96
0.50	1.00	0.21	0.86	0.38	0.39	0.43	0.82	1.23	3.97	0.18	1.87	2.10	2.65
0.60	1.10	0.21	0.86	0.35	0.39	0.47	0.86	1.28	4.17	0.19	1.87	2.30	2.42
0.70	1.19	0.21	0.86	0.32	0.39	0.51	0.90	1.33	4.36	0.19	1.87	2.48	2.24
0.80	1.27	0.21	0.86	0.30	0.39	0.55	0.93	1.36	4.53	0.20	1.87	2.65	2.09
0.90	1.35	0.21	0.86	0.29	0.39	0.58	0.97	1.40	4.69	0.20	1.87	2.81	1.98
1.00	1.42	0.21	0.86	0.27	0.39	0.61	1.00	1.43	4.84	0.21	1.87	2.97	1.87

Age 2 (7.43 months)

Froude	velocity	limb length	NPP	t_c	L_1	L_2	SL	SF	dSL	dSF	dL_1	dL_2	dt_c
0.10	0.56	0.33	0.86	0.87	0.49	0.24	0.73	0.77	2.25	0.14	1.51	0.75	4.77
0.20	0.80	0.33	0.86	0.61	0.49	0.34	0.83	0.96	2.56	0.17	1.51	1.06	3.37
0.30	0.98	0.33	0.86	0.50	0.49	0.42	0.91	1.07	2.80	0.20	1.51	1.29	2.75
0.40	1.13	0.33	0.86	0.43	0.49	0.49	0.98	1.16	3.00	0.21	1.51	1.49	2.38
0.50	1.26	0.33	0.86	0.39	0.49	0.54	1.03	1.22	3.18	0.22	1.51	1.67	2.13
0.60	1.38	0.33	0.86	0.35	0.49	0.59	1.08	1.27	3.34	0.23	1.51	1.83	1.95
0.70	1.49	0.33	0.86	0.33	0.49	0.64	1.13	1.32	3.48	0.24	1.51	1.98	1.80
0.80	1.60	0.33	0.86	0.31	0.49	0.69	1.18	1.36	3.62	0.25	1.51	2.11	1.69
0.90	1.69	0.33	0.86	0.29	0.49	0.73	1.22	1.39	3.75	0.25	1.51	2.24	1.59
1.00	1.78	0.33	0.86	0.27	0.49	0.77	1.26	1.42	3.87	0.26	1.51	2.36	1.51

Note:
Age 1 is Infant 1 at 6.97 months; Age 2 is Infant 1 at 7.43 months
Velocity is forward velocity in m/s
NPP is the limb natural pendular period in seconds
t_c is stance duration in seconds
L_1 is the distance traveled during stance phase (step length) in meters
L_2 is the distance traveled during swing phase in meters
SL is stride length in m
SF is stride frequency in s^{-1}
dSL is relative stride length
dSF is dimensionless stride frequency
dL_1 is dimensionless step length
dL_2 is dimensionless swing length
dt_c is dimensionless stance duration

FIGURES

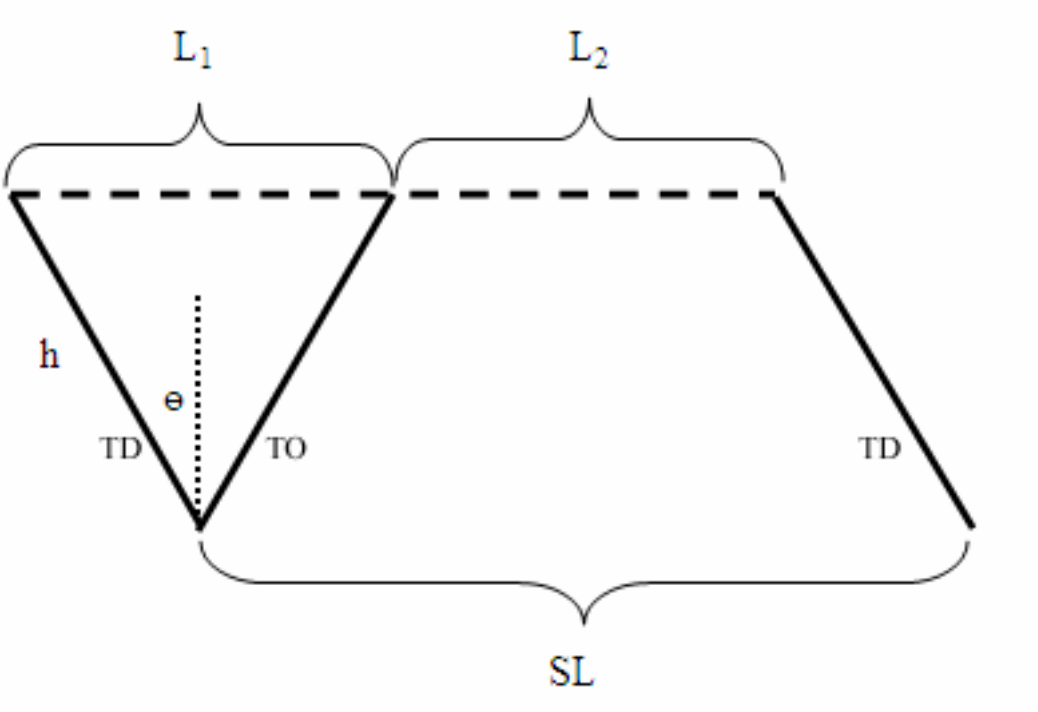


Figure 3.1. Diagram of locomotor model after Reynolds (1987)

The hindlimb in the locomotor model is represented by a single rigid element of length h (solid black lines). A stride begins with the hindlimb protracted (θ) at touchdown (TD). Over stance phase, the limb moves through an angular excursion of 2θ and at toe-off (TO) the hip (proximal end of the hindlimb) has moved a distance of L_1 (step length). The distance traveled during swing phase (the time between TO and the next TD) is L_2. The sum of L_1 and L_2 is equal to the distance traveled over the entire stride (stride length; SL). This distance should be equivalent if measured at the ankle or the hip. See text for further details.

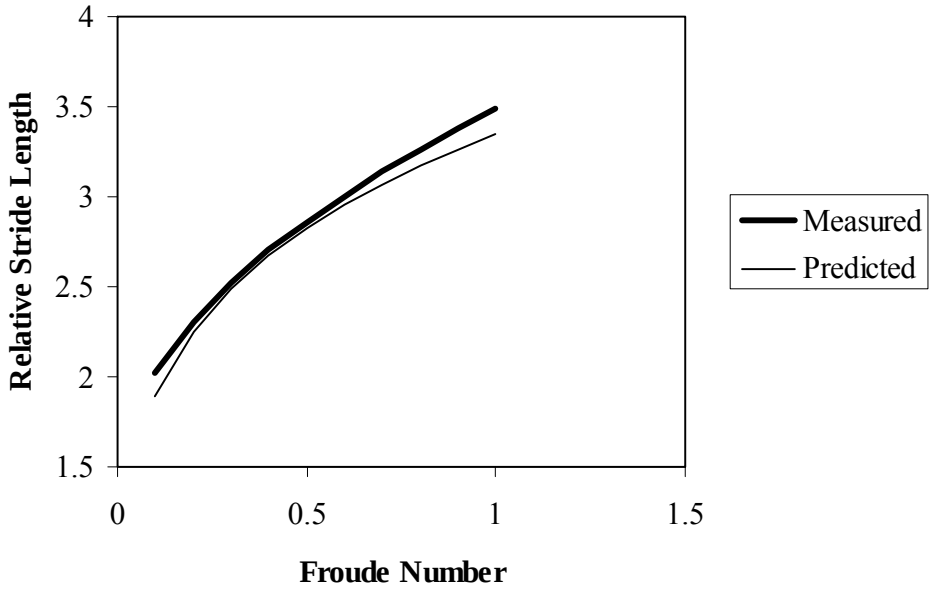


Figure 3.2. Test of model accuracy for predicting relative stride lengths of a male baboon (data from Polk, 2001, unpublished data).

Heavy line represents actual relative stride lengths at a given Froude number for a male baboon from Polk (2001). Thin line represents the relative stride lengths predicted for this individual by the locomotor model based on its limb inertial properties (Polk, unpublished data).

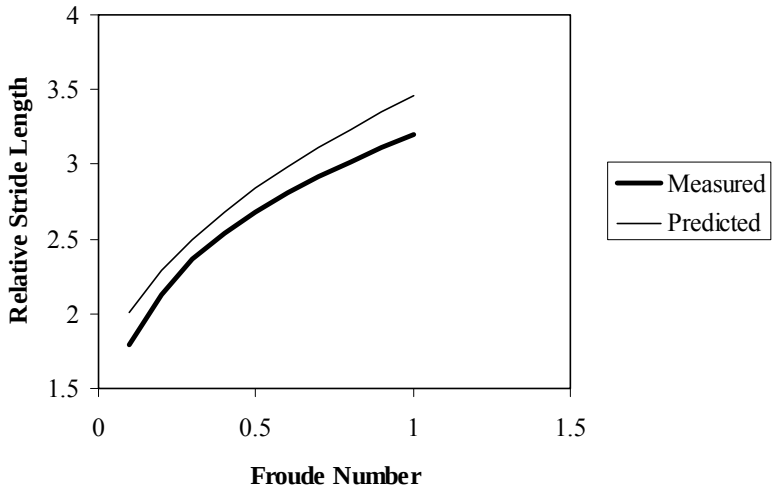


Figure 3.3. Test of model accuracy for predicting relative stride lengths of a male patas monkey (data from Polk, 2001, unpublished data).

Heavy line represents actual relative stride lengths at a given Froude number for a male patas monkey from Polk (2001). Thin line represents the relative stride lengths predicted for this individual by the locomotor model based on its limb inertial properties (Polk, unpublished data).

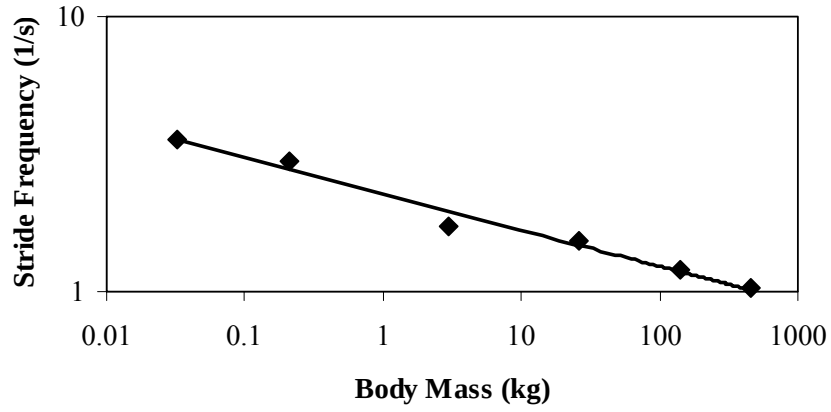


Figure 3.4. Predicted stride frequencies at the trot-gallop transition for quadrupedal mammals.

Data for limb lengths and body masses for quadrupedal mammals are from Hoyt et al. (2000). Predicted stride frequencies are plotted against increasing body mass on logarithmically transformed axes. Predicted stride frequencies decrease with increasing body mass according to the following equation: $y = 2.26x^{-0.13}$.

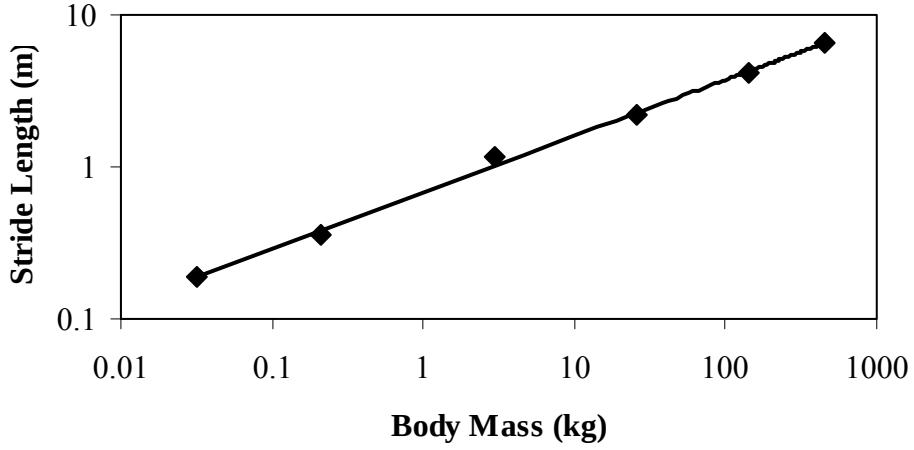


Figure 3.5. Predicted stride lengths at the trot-gallop transition for quadrupedal mammals.

Data for limb lengths and body masses for quadrupedal mammals are from Hoyt et al. (2000). Predicted stride lengths are plotted against increasing body mass on logarithmically transformed axes. Predicted stride lengths increase with increasing body mass according to the following equation: $y = .676x^{0.37}$.

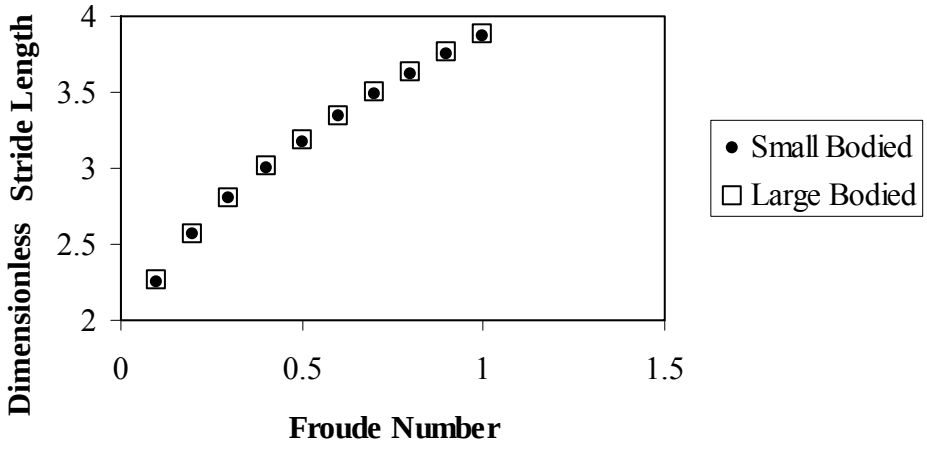


Figure 3.6. Dynamic similarity of predicted relative stride lengths in two mammalian quadrupeds.

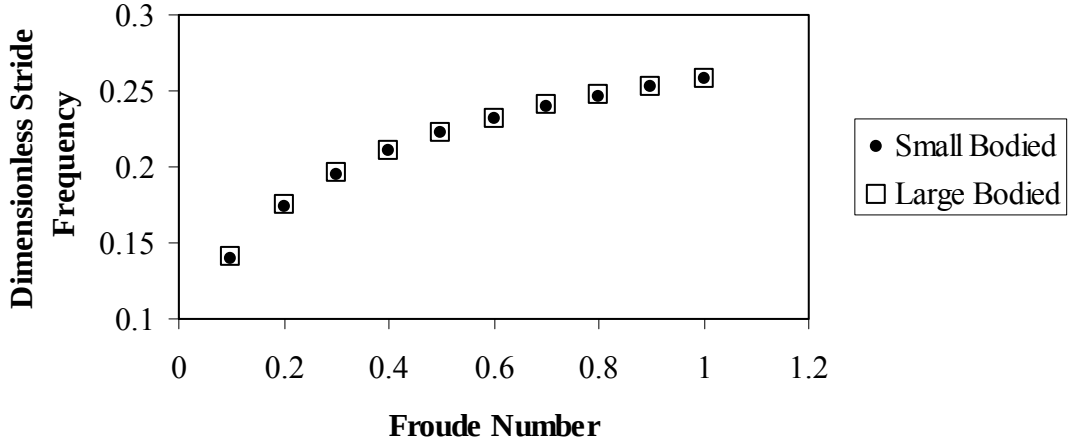


Figure 3.7. Dynamic similarity of predicted dimensionless stride frequencies in two mammalian quadrupeds.

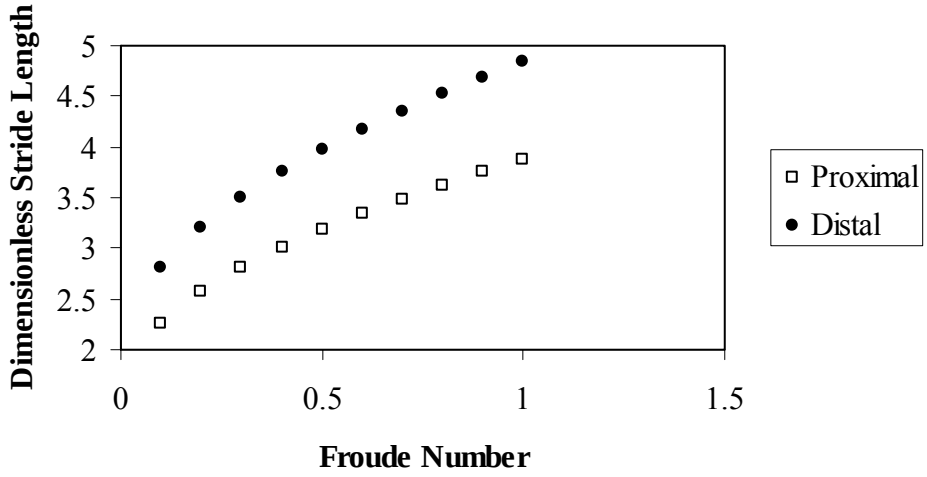


Figure 3.8. Effects of mass distribution on predicted dimensionless stride lengths.

The infant baboon's predicted relative stride lengths at its young age, when mass was relatively more distal, is represented by closed circles, and predicted stride lengths at its older age, when limb mass was more proximal, is represented by open squares. Proximal refers to the individual with the proximal limb mass concentration (7.43 months) and distal refers to the individual with more distal limb mass (6.97 months).

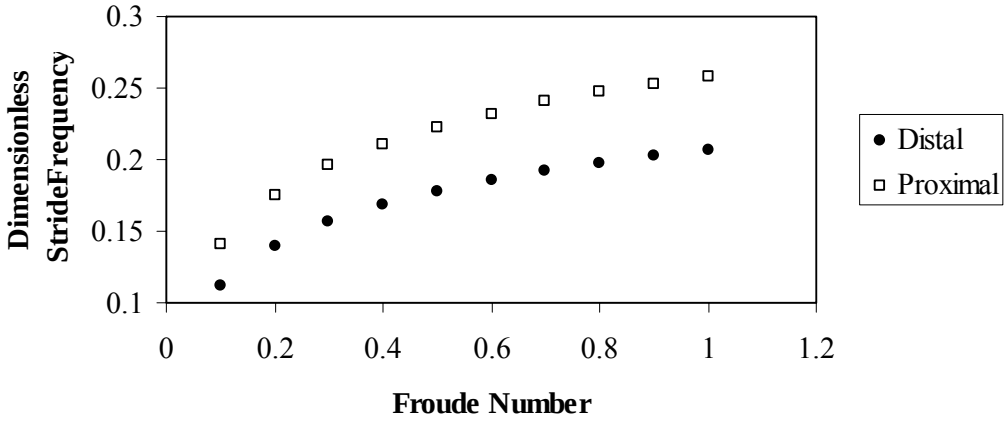


Figure 3.9. Effects of mass distribution on predicted dimensionless stride frequencies.

Symbols as in Figure 3.8.

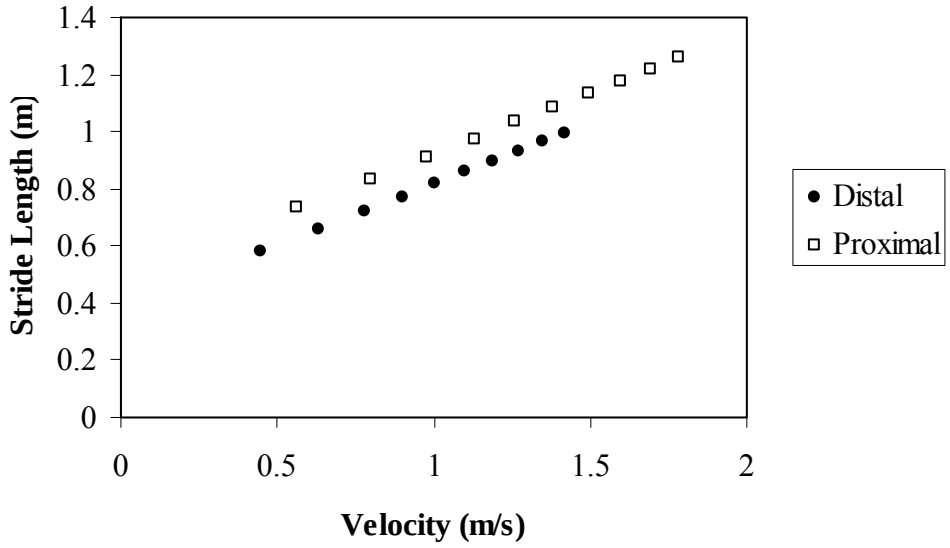


Figure 3.10. Effects of mass distribution on predicted raw stride lengths.

Symbols as in Figure 3.8.

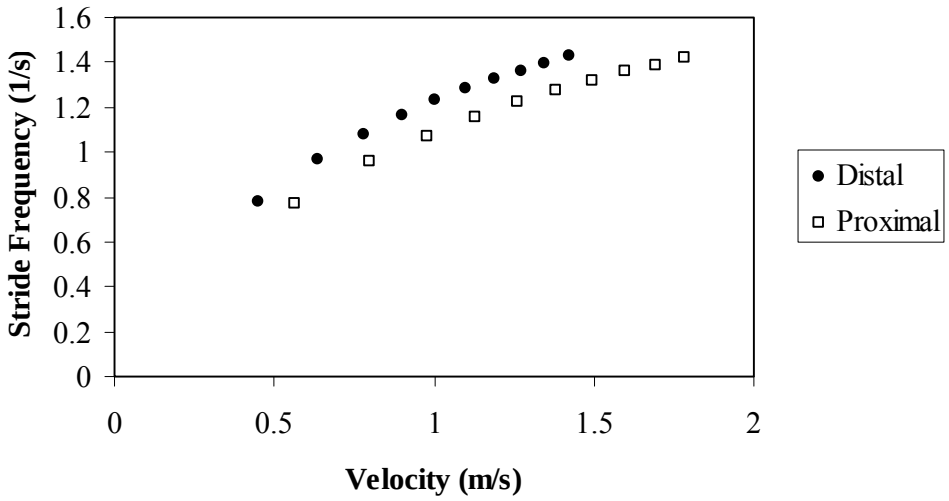


Figure 3.11. Effects of mass distribution on predicted raw stride frequencies.

Symbols as in Figure 3.8.

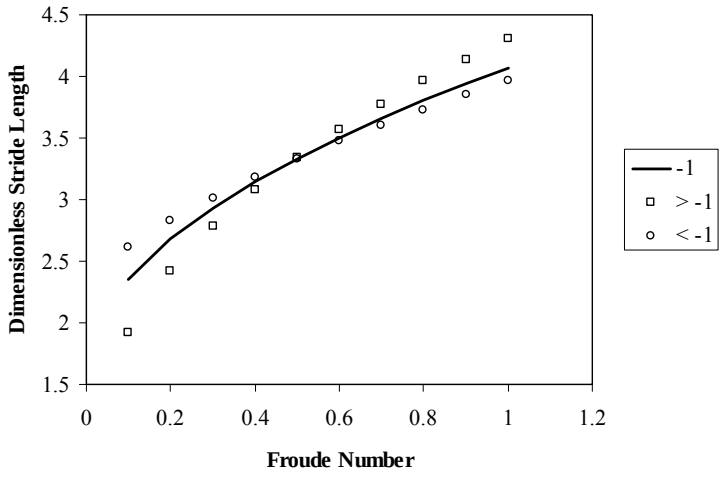


Figure 3.12. Effects of violating stance duration assumptions on predicted dimensionless stride lengths.

Solid line is dimensionless stride lengths predicted when factor a in equation 3.7 is equal to -1. If factor a is greater than -1 (open squares) dimensionless stride lengths increase at a higher rate with increasing Froude numbers. If factor a is less than -1 (open circles), relative stride lengths increase at a lower rate with increasing Froude numbers.

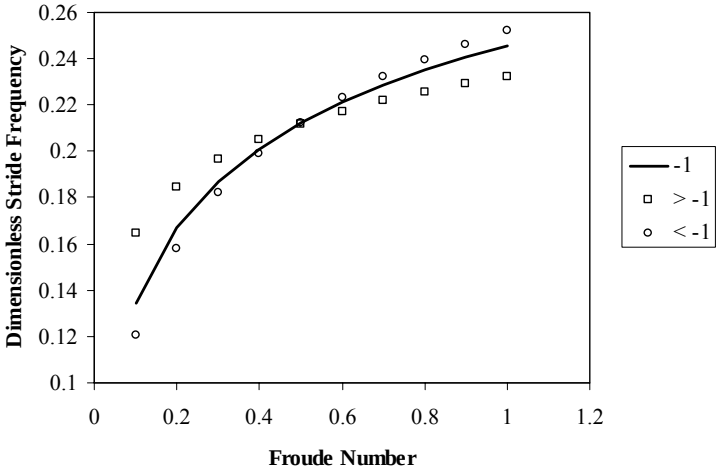


Figure 3.13. Effects of violating stance duration assumptions on predicted dimensionless stride frequencies.

Solid line is dimensionless stride frequency predicted when factor a in equation 3.7 is equal to -1. If factor a is greater than -1 (open squares) dimensionless stride frequencies increase at a lower rate with increasing Froude numbers. If factor a is less than -1 (open circles), dimensionless stride frequencies increase at a higher rate with increasing Froude numbers.

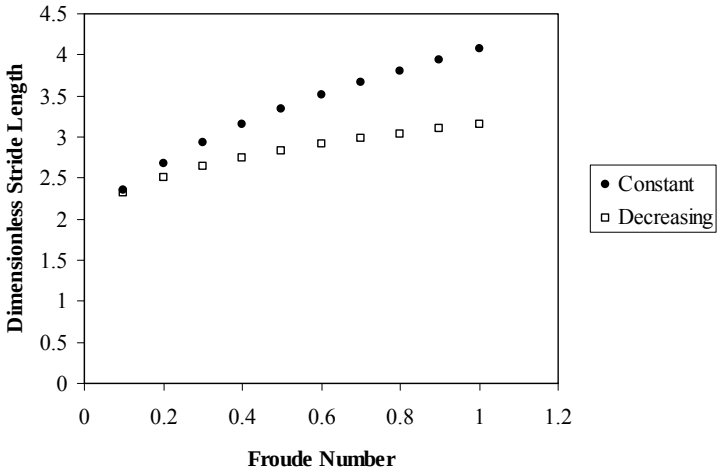


Figure 3.14. Effects of violating swing phase assumptions on predicted dimensionless stride lengths. If swing phase decreases with increasing Froude numbers (open squares), dimensionless stride lengths will increase at a lower rate compared to the increase in dimensionless stride length with increasing Froude numbers when swing phase is constant (closed circles).

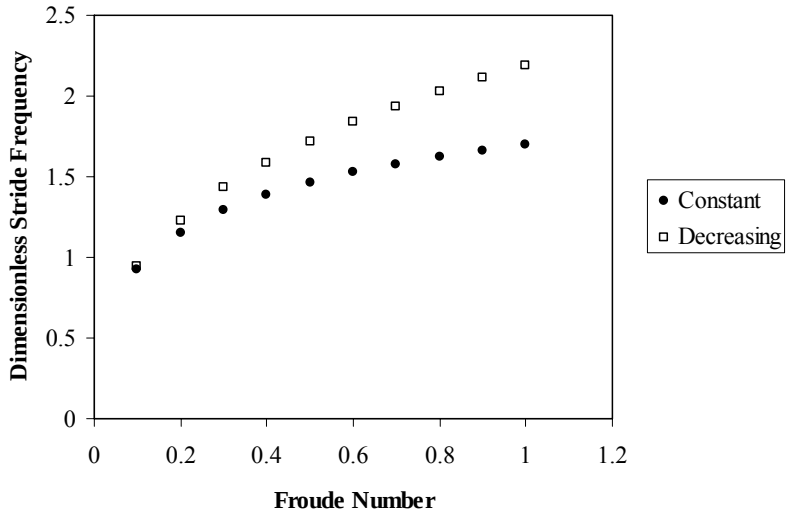


Figure 3.15. Effects of violating swing phase assumptions on predicted dimensionless stride frequencies. If swing phase decreases with increasing Froude numbers (open squares), dimensionless stride frequency will increase at a higher rate compared to the increase in dimensionless stride frequency with increasing Froude numbers when swing phase is constant (closed circles).

CHAPTER 4

The Effects of Ontogenetic Changes in Limb Mass Distribution on the Ontogeny of Spatio-temporal Kinematics in *Papio cynocephalus*

INTRODUCTION

Based on the locomotor model described in Chapter 3, limb mass distribution should have significant impacts on an individual's locomotor kinematics. Specifically, it is possible differences in limb inertial properties may explain known differences in spatio-temporal kinematics in primates compared to non-primate quadrupeds.

The locomotor model predicts that individuals with relatively more distally concentrated limb mass should walk and run with low dimensionless stride frequencies and long dimensionless strides. To achieve these kinematic characteristics, these individuals would also walk with long dimensionless stance and swing durations as well as long dimensionless step lengths.

Primate quadrupeds have been described as using this combination of characteristics by several researchers (Alexander and Maloiy, 1984; Reynolds, 1987; Vilensky and Larson, 1989; Demes et al., 1990; Schmitt; 1998; Schmitt, 1999; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002). If the predictions made by the locomotor model are supported by empirical evidence, then it is likely that primate quadrupedal kinematics may largely be explained by their unique distal limb mass concentrations used to control their grasping extremities.

A connection between primate quadrupedal kinematics and their grasping extremities demonstrates how selection has acted on the locomotion of primates in general. The earliest primates would have evolved grasping extremities for use in an arboreal, and perhaps a fine branch, niche. Their unique kinematic characteristics would then have been a necessary byproduct of this original adaptation.

Additionally, several researchers have described how these locomotor characteristics benefit arboreal quadrupedalism on small diameter branches (see Demes et al., 1990; Larson, 1998; Schmitt, 1998; Schmitt, 1999; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002; Schmitt, 2003). A connection between distal limb mass distributions and grasping hands and feet complements the small branch niche hypothesis. Grasping hands and feet likely evolved in a small branch niche, and the kinematic characteristics associated with this adaptation would have also helped primate quadrupeds maintain safe arboreal travel. Importantly, though, a connection between distal limb mass distributions and locomotor kinematics would provide an explanation for why primate quadrupeds continue to use these kinematics while walking and running on the ground (especially primates who are dedicated terrestrial quadrupeds), since all extant primates have grasping hands and feet.

A sample of infant baboons (*Papio cynocephalus*) was used to test the predicted relationship between limb mass distribution and spatio-temporal kinematics. The infant baboon sample offers a "natural experiment" because their limb mass distributions change with age (see Chapter 2). The infant baboons have relatively more distal limb mass concentrations at young ages, and this mass distribution migrates proximally with

age. Therefore, it is possible to examine how their locomotor kinematics change with their proximal migrations of limb mass distribution.

Hypotheses

The infant baboons will be tested for ontogenetic dynamic similarity. If the infant baboons follow the predictions made by the locomotor model, they should not walk with dynamic similarity as they age. They should use lower dimensionless stride frequencies and longer dimensionless stride lengths at a given dimensionless velocity at their youngest ages. Additionally, infant baboons should use longer dimensionless swing and stance durations, as well as longer dimensionless step lengths at a given dimensionless velocity at these young ages, when their limb mass is most distally concentrated.

In addition to examining whether or not the infant baboons walk with ontogenetic dynamic similarity, kinematics will be examined at trot-gallop transition velocities. Researchers have noted distinct trends in kinematic variables with increasing body size at the trot-gallop transition velocity (see Heglund and Taylor, 1974, 1988). If limb mass distribution influences kinematics in infant baboons, then the relationships between body size and kinematics at the trot-gallop transition should be weaker than those found in geometrically similar mammals (see Heglund and Taylor, 1974, 1988). The relationship would be weakened because at young ages, when Heglund and Taylor (1974, 1988) would predict the individuals to use relatively high stride frequencies because of their small body mass, the infant baboons would be using relatively lower stride frequencies due to their distal limb mass concentrations.

MATERIALS AND METHODS

The sample used in the analysis of ontogenetic changes in locomotor kinematics is the same as that used for the analysis of ontogenetic changes in limb mass distribution patterns (Chapter 2). Four infant baboons (*Papio cynocephalus*) were obtained from the Southwest Foundation for Biomedical Research (SFBR) from a population rejected by their mothers and placed in the SFBR nursery. Infant baboons were housed at the University of Texas Animal Resource Center using methods approved by both the University of Texas institutional animal care and use committee (IACUC) and the SFBR IACUC.

Three-dimensional kinematic data were obtained from each infant baboon at regular intervals during development (Table 4.1). Kinematic data were collected on each infant baboon two days before or after data were collected on limb inertial properties (see Chapter 2). Infant baboons were allowed to walk and run at freely chosen velocities through a lexan tunnel made up of three removable sections (2x3x4 feet each). Two or three sections were used depending on each infant baboon's body size at the time of data collection (on some days, 2 sections were used, but were separated by approximately 2 feet). At young ages, animals were encouraged to walk and run the length of the tunnel using toys. As soon as they began eating solid foods (approximately three months of age), the infant baboons were encouraged to walk and run the length of the tunnel using food rewards. Prior to tunnel entry, spherical reflective markers (14 mm; Oxford Metrics, Inc.) were glued to the major joints of the forelimbs and hindlimbs of each infant baboon (hip, knee, ankle, shoulder, elbow, knee). The placement of each marker was

consistent with the segment definitions used for inertial property data collection (see Chapter 2).

Three dimensional marker trajectories were captured for one side of the body during each locomotor trial using a 5 camera Vicon 250 data acquisition system (Oxford Metrics, Inc.) capturing data at 60 Hz. Camera placement was consistent for all data collection sessions. Prior to each data collection session, cameras were calibrated as per the Vicon 250 instruction manual using both static and dynamic calibrations. The calibration instruments were the Vicon clinical L-frame (static) and the 500 mm wand (dynamic). Calibration residuals were between 0.25 and 0.60 mm for all cameras and for all data collection sessions. Although markers were placed on both sides of the body, cameras were placed in an arc on only one side of the tunnel in order to maximize the calibrated viewing volume and maximize the capabilities of the system to track the three dimensional positions of the relatively small (14 mm) markers (see Figure 4.1). One problem with using a passive reflective marker based system is that the markers must remain relatively clean throughout a data collection session. This was not always possible for the infant baboons, so having five cameras tracking one side of the body also minimized the possibility that a dirty marker would be lost completely.

In addition to the Vicon system, video data of each trial were collected using a digital video camera (JVC-GRDVL9800E) capturing data at 60 frames per second. The video data were routed through a frame counter (manufactured by Oxford Metrics, Inc.) and transferred to a Hi-8 analog tape. This transfer allowed the frame counter to be burned onto the image so that each kinematic trial could later be synchronized to Vicon-generated data.

Marker trajectories were reconstructed using Vicon Workstation software. Kinematics data were processed using Vicon Bodybuilder software. If there were any gaps in marker trajectories of less than 10 frames (<0.17 s), the gaps were filled using the Vicon interpolation algorithm. Three dimensional marker positions were then exported into Microsoft Excel for the remainder of data processing.

Frame numbers for touchdowns and lift-offs of the forelimbs and hindlimbs of both sides of each infant baboon during each locomotor trial were obtained from the video data. Touchdown for a limb was defined as the first frame where a hand or foot accepted body weight. Lift-off was defined as the first frame where a hand or foot that was in ground contact does not support any body weight. A locomotor trial was accepted for use if the individual was not obviously accelerating or decelerating during the trial and if there was at least one visible stride before and after the stride of interest. All walks and runs were also analyzed for symmetry. Symmetry is the time between a limb's touchdown, and the next touchdown of the contralateral limb of the same girdle as a percentage of stride duration. In normal, steady-state walks and runs, this value should be 50 (see Hildebrand, 1966). In practice, symmetry values between 45 and 55 are viewed as acceptable for symmetrical walk and runs (see Cartmill et al., 2002; Shapiro and Raichlen, in press). All walking and running trials with symmetry values outside of this range were rejected.

Variables

Each stride's duration (seconds) was defined as the elapsed time between the touchdown of the hand or foot on the side facing the camera (ipsilateral) to the next

touchdown of that hand or foot. Stride frequency (Hz) was calculated as the reciprocal of stride duration. Stance duration (seconds) was calculated as the elapsed time between limb touchdown and lift-off. Swing duration (seconds) was calculated as the elapsed time between limb lift-off and touchdown. Stride length (m) was calculated in two ways: 1) the distance traveled by the ankle or wrist marker during a given stride and 2) the distance traveled by the hip or shoulder marker during a given stride. These data do not differ significantly (see Fig. 4.2a & b), so the ankle and wrist marker stride lengths were used in this study to remain consistent with the literature. Velocity (m/s) was calculated as the quotient of stride length and stride duration. Step length (m) was calculated as the distance traveled by the hip or shoulder marker during stance phase.

Limb angles were calculated for each stride as the angle between a line connecting the hip marker with the ankle marker, or a line connecting the shoulder and wrist markers, and a vertical line passing through the hip or shoulder marker (see Fig. 4.3; after Larson et al., 2000, 2001; Shapiro and Raichlen, in press). Limb protraction is the angle at touchdown, limb retraction is the angle at lift-off and total limb excursion is the sum of the absolute values of the protraction and retraction angles for a given stride. Zero degrees indicates the limb is perpendicular to the ground and 90 degrees would indicate that the limb is parallel to the ground. Positive angles indicate the limb is protracted and negative angles indicate the limb is retracted.

Forelimb vs. Hindlimb

Most research into mammalian quadrupedal kinematics has focused on single limb kinematics (e.g. Heglund and Taylor, 1974; Schmitt, 1994). In this study kinematic

variables of interest were calculated for both the forelimb and the hindlimb on one side of the body for each stride. The values obtained for the forelimb and hindlimb for each variable were then compared at a given velocity to determine whether or not the infant baboons' kinematics could be generalized by a single limb analysis.

Dimensionless numbers

In order to compare the infant baboons intra-individually and inter-individually as they age, changes in size must be taken into account. The method used to correct for differences in size at a given age for each individual was to test for dynamic similarity in kinematic variables. In this study, dimensionless velocity was calculated as the square root of the Froude number after Hof (1996; see also Aerts et al., 2000; Polk, 2002). Dynamic similarity is only possible when the subjects are geometrically similar (see Alexander and Jayes, 1983). Hindlimb length (h) was used as the characteristic size variable since the analysis of ontogenetic changes in limb length meets the criterion of isometric increases in limb length with increasing body size in this sample of infant baboons (see Chapter 2). Stride frequencies were corrected for size after Hof (1996; see also Zjilstra, 1996; Aerts et al., 2000):

$$dSF = \frac{SF}{\sqrt{\frac{g}{h}}} \qquad (3.1)$$

Spatial variables (L; step length and stride length) were made dimensionless after Alexander and Jayes (1983; see also Hof, 1996; Aerts et al., 2000):

$$dL = \frac{L}{h} \qquad (3.2)$$

All time variables (T: stance duration and swing duration) were made dimensionless after Hof (1996):

$$dT = \frac{T}{\sqrt{\frac{h}{g}}}. \qquad (3.3)$$

Changes with increasing body mass

Since much of the literature has focused on changes in kinematics at the trot-gallop transition (see Heglund and Taylor, 1974; Hoyt and Taylor, 1981; Heglund and Taylor, 1988; Wickler et al. 2003), kinematic variables were compared within individuals at this physiologically equivalent point. The trot-gallop transition proves problematic when applied to primates because in general, primates do not use a running trot (Dagg, 1973; Preuschoft and Gunther, 1994; Larson, 1998). Additionally, primates may not transition to a gallop for the same reasons as do other mammals (Demes et al., 1994, 1998). Despite these problems, it is useful to examine how the infant baboons' kinematics differ ontogenetically at this velocity.

Trot-gallop transition velocities were predicted from McMahon (1975; $V_{tg}=(5.5M^{.24})*3.6$) and the stride frequency of each individual at this transition was predicted from the regression line relating stride frequency and velocity for each individual at each age (after Polk, 2001). 95% confidence intervals for these values were calculated using the 95% confidence intervals for the slope and intercept of the regression line relating stride frequency and velocity. Although obviously not a very robust analysis, this portion of the study will serve as an important check on the dimensionless

numbers analysis. If limb inertial properties play a significant role in determining stride frequency, and limb mass is relatively more distal at young ages when body mass is also small, then it is expected that changes in stride frequency at the trot-gallop transition with increasing body mass should be relatively weak (the 95% confidence limits at each body mass should overlap).

Grouping

Most ontogenetic studies of locomotion examine changes across age categories determined by either body size differences or broad behavioral changes (e.g. Vilensky et al., 1988; Dunbar and Badam, 1998; Irschick and Jayne, 2000; Wells and Turnquist, 2001). These categorizations are not as useful in this study, because, as described above, the purpose of the present project is not simply an ontogenetic analysis, but asks specific questions about the impacts of ontogenetic changes in limb inertial properties on locomotion. Therefore, individuals must be grouped based on their limb inertial properties, and these groupings may or may not conform to arbitrary age classes. Additionally, although limb mass distributions may differ between two ages, limb kinematics during swing phase may negate these differences (see Myers and Steudel, 1997; Raichlen, 2004) and therefore affect the results of a study employing arbitrary age distinctions.

The method used to create age groupings began with the calculation of an infant baboon's limb inertial properties at each frame for each stride. Since the limb is modeled as a physical pendulum, limb flexion will reduce the limb's natural pendular period (Hildebrand, 1985; Myers and Steudel, 1997; Raichlen, 2004). Therefore, the minimum

limb dimensionless NPP ($dNPP_{min}$) calculated for each trial during swing phase was used as the inertial property of interest for groupings. It is expected that, even though the infant baboons' limb inertial properties change in a regular way with age (see Chapter 2), individuals will not differ significantly in $dNPP_{min}$ at all ages. The same amount of flexion has a proportionately greater impact on an individual with a more distal concentration of limb mass compared to an individual with a more proximal concentration of limb mass (see Fig. 4.4).

Statistical analysis

For each infant baboon at each age, Pearson-moment correlations between $dNPP_{min}$ and velocity were tested for significance. If there were no correlations between $dNPP_{min}$ and velocity for all ages, then comparisons between mean $dNPP_{min}$ at different ages were performed using single factor ANOVA with a Tukey-Kramer post-hoc tests to correct for multiple comparisons. If correlations were present between $dNPP_{min}$ and velocity at any age within an individual, comparisons of $dNPP_{min}$ across ages were carried out using ANCOVA with Tukey-Kramer post-hoc tests to correct for multiple comparisons. Prior to performing an ANCOVA, data sets were checked for homogeneity of slopes (see Sokal and Rohlf, 1995). ANCOVA was also used if some ages had a variable correlated with velocity, while others did not (see Polk, 2001). All ages for an individual that did not significantly differ in $dNPP_{min}$ were grouped together. These groupings were then used for further analyses of the impacts of limb inertial properties on locomotor kinematics.

For each locomotor variable, a similar approach was used. First, Pearson-moment correlations were performed between each variable and velocity (and dimensionless velocity). If the correlation was not significant, then locomotor variables were compared between different groups using single-factor ANOVA with Tukey-Kramer post-hoc tests to correct for multiple comparisons. If correlations were significant, ANCOVA was performed with Tukey-Kramer post-hoc tests to accommodate multiple tests. If an ANCOVA was used, least-squares means (LSmeans) and their 95% confidence limits were calculated to aid comparisons. All statistical tests were performed using SAS version 8.0 (SAS institute, Inc., 2003).

RESULTS

Groupings

The results for the analysis of changes in limb mass distribution during locomotion indicate that Infant 1 clusters into two groups: less than 5 months and greater than 5 months (Table 4.2). There are no significant differences within each group, but significant differences exist between the two groups (Table 4.2).

Values of $dNPP_{min}$ for Infant 2 also cluster into two groups (Table 4.3). The transition to smaller values occurs after 4 months for this individual (Table 4.3). Again, within the two groups, values of $dNPP_{min}$ do not differ significantly (Table 4.3) with two exceptions. At 2.83 months, mean $dNPP_{min}$ is significantly larger than at 3.67 months. Because this value is larger than at 2.03 months, and because 2.03 months does not differ from $dNPP_{min}$ at 3.67 months, all three of these ages were grouped together. $dNPP_{min}$ in

this infant at 4.97 months is significantly smaller than it is at 5.53 months. Since the $dNPP_{min}$ was lower at a younger age in this individual, values for 4.97 months were grouped with the older ages into Group 2.

Values of $dNPP_{min}$ for Infant 3 also cluster into two major groups (Table 4.4), with the transition to smaller values occurring after 5 months of age. Within each of the two groups, values of $dNPP_{min}$ do not significantly differ (Table 4.4).

Surprisingly, the values of $dNPP_{min}$ for Infant 4 do not differ significantly among the three sampled age ranges (Table 4.5). The results for Infant 4 should be treated with caution, as sample sizes are much lower in this individual compared to Infants 1-3 (see Table 4.1). Regardless of the low sample sizes, the fact that Infant 4's $dNPP_{min}$'s did not differ significantly over the three sampled ages allows Infant 4 to act as a control for the effects of neurological ontogeny on spatio-temporal kinematics. If Infant 4 undergoes the same changes in kinematics as Infants 1-3 despite her similar inertial properties, then support for a connection between limb mass distribution and kinematics will be weakened considerably.

For the remainder of this study, there will be two groupings for Infants 1-3 based on the results of this analysis. Group 1 will include all of the youngest ages that do not differ significantly in $dNPP_{min}$, and Group 2 will include all of the oldest ages that do not differ significantly in $dNPP_{min}$. For Infant 4, three groups will be assigned, one for each sampled age.

Forelimb versus hindlimb

One way to simplify the analysis of quadrupedal kinematics has been to focus on a single limb's (e.g. hindlimb) kinematics and generalize those results to the other limb. It is important to verify the assumption that forelimb and hindlimb kinematics are similar before simply focusing on one limb. To do this, a comparison was made of how major variables change with velocity in both the forelimb and the hindlimb in the infant baboons. The analysis was performed on the entire, combined sample of infant baboons.

For the four major variables included in this analysis (SL, SF, t_c, and t_s) forelimbs and hindlimbs do not differ significantly in the infant baboons (Figs. 4.5-4.8; Table 4.6). Because of this overall similarity in forelimb and hindlimb kinematics across all ages in the infant baboon sample, the remainder of the results will be presented for the hindlimb only.

Assumptions of the locomotor model

Two major assumptions used in the locomotor model (Chapter 3) were that stance phase would decrease in direct proportion to increases in velocity and that swing phase duration would remain relatively constant with increasing velocity. In all individuals at most ages, the 95% confidence limits of the slopes of the regression lines relating stance duration and velocity include -1.0, indicating a directly proportional relationship (Table 4.7). There are four instances where the 95% confidence limits for the slopes of these regression lines do not quite overlap with -1.0, although they are very close. In these cases, the slope is slightly steeper than -1.0, indicating stance duration decreases slightly

more steeply than velocity. In general, however, this assumption of the model is not violated by this sample of infant baboons.

Swing duration decreases with increasing velocity in all infant baboons at all ages (Fig. 4.8; Table 4.8), indicating the infant baboons violate the assumption of constant swing phase duration. This violation will affect the rate of change of stride frequencies and stride lengths with velocity. It is the slope of the line relating swing duration and velocity that affects modeled predictions (see Chapter 3), so if the slopes do not differ between groups, then the model's predictions are still valid. The 95% confidence limits for the slopes of the least-squares regression lines (in log space) overlap between Groups 1 and 2 for each individual (Table 4.8). This similarity of slopes indicates that the decrease in swing duration with increasing velocity will not affect modeled predictions because the rates of change are similar among all sampled ages.

Temporal variables

Raw stride frequency

For Infant 1, Group 1 used slightly higher stride frequencies at a given velocity compared to Group 2 (Fig. 4.9a; Table 4.9). For Infant 2, Group 1 used significantly lower stride frequencies at a given velocity compared to Group 2 (Fig. 4.9b; Table 4.9). Stride frequencies at a given velocity did not differ significantly between Groups 1 and 2 for Infant 3 (Fig. 4.9c; Table 4.9). Finally, although there are significant inter-group differences for Infant 4 (stride frequencies decrease with increasing body size), her velocities did not overlap, so this analysis should be treated with caution (Fig. 4.9d; Table

4.10). Regression statistics for raw stride frequency changes with velocity for all infant baboons at all ages can be found in Table 4.11.

Because Group 1 individuals are smaller in body size than Group 2 individuals (see Table 4.11), these results suggest that body size alone does not predict stride frequency in this sample. Heglund and Taylor (1974, 1988) suggested that smaller individuals use higher stride frequencies at preferred velocities as well as at the walk-trot and trot-gallop transitions. Infants 1 and 2 did not use higher stride frequencies at smaller body sizes, as predicted by Heglund and Taylor (1974, 1988; Strang and Steudel, 1990), and Infant 1's stride frequencies at smaller body sizes were only slightly higher. Had the infant baboons followed the predictions of Heglund and Taylor (1974, 1988), they should have used higher stride frequencies at younger ages.

As described above, based on the work of Heglund and Taylor (1974), stride frequencies at the trot-gallop transition are expected to decrease with increasing body size. For all infant baboons, the 95% confidence limits for predicted stride frequencies at their trot-gallop transitions overlap at all ages and body masses (Fig. 4.10). These data indicate that stride frequencies at the trot-gallop transition do not decrease significantly in this sample as individuals nearly double their body masses. Again, differences within individual infant baboon stride frequencies do not match predictions made by Heglund and Taylor (1974, 1988) based on their body mass differences.

Relationship between dimensionless stride frequency and age

The comparisons of dimensionless stride frequencies among the infant baboons provides a better picture of why body mass alone does not predict the relationship between stride frequency and velocity in this sample.

Table 4.12 gives the results of an ANCOVA comparing the relationship between dimensionless stride frequency and dimensionless velocity in the two age groups for Infants 1-3. Group 1 for Infant 1 used significantly lower stride frequencies compared to Group 2 (Fig. 4.11a). The LSmeans are significantly different, and the LSmean for Group 1 is significantly lower than the LSmean for Group 2 (Table 4.12). LSmeans do not differ significantly between different ages within each group for Infant 1, indicating that indeed, groupings based on "functional" inertial properties are valid (Table 4.13). Dimensionless stride frequencies at 4.73 months fall between the data for the two age groupings and do not differ significantly from either of the groups (younger or older).

Infant 2 also used significantly lower dimensionless stride frequencies at a given dimensionless velocity at younger ages (Fig. 4.11b). Group 1 for this individual has significantly lower LS means than Group 2 (Table 4.12). LS means generally do not differ significantly between different ages within each group (Table 4.14).

Infant 3 shows a slightly different pattern for the changes in dimensionless stride frequencies at a given dimensionless velocity. At low dimensionless velocities, Group 1 for Infant 3 uses lower dimensionless stride frequencies at a given dimensionless velocity compared to Group 2 (Fig. 4.11c). This difference disappears at higher dimensionless velocities as the slope of this relationship for Group 1 increases. Because the slopes of these two groups are not parallel (Fig. 3.29c), an ANCOVA could not be performed over

the entire velocity range (see Sokal and Rohlf, 1995). LSmeans were, however calculated for the lower velocity range, and these values are significantly lower for Group 1 in this individual (Table 4.12). LSmeans do not differ significantly between different ages within each group (Table 4.15).

Because the analysis of functional inertial properties in Infant 4 did not reveal significant differences between different ages, dimensionless stride frequencies were compared between all sampled ages. LSmeans did not differ significantly between the different ages for this individual (Fig. 4.11d; Table 4.16).

The infant baboons that did group by hindlimb NPP (Infants 1-3) were combined so that all Group 1 individuals were compared to all Group 2 individuals. Dimensionless stride frequencies were significantly lower in the combined Group 1 individuals compared to the combined Group 2 individuals (Fig 4.12; Table 4.17).

Dimensionless swing and stance durations

Because differences in stride frequencies are apparent as an infant baboon's limb inertial properties change, the extent to which these differences are caused by changes in stance phase and swing phase was examined.

Infant 1 did not show significant between-group differences in dimensionless stance durations after dimensionless velocity had been taken into account (Fig. 4.13a; Table 4.18). Dimensionless stance durations in Infants 2 and 3 are significantly longer in Group 1 compared to Group 2 (Fig. 4.13b&c; Table 4.18). Dimensionless stance duration does not differ significantly among the sampled ages in Infant 4 (Fig. 4.13d; Table 4.19).

Dimensionless swing phase duration is significantly longer when limb mass is concentrated most distally (Group 1) in the three individuals who show a change in functional inertial properties (Infants 1-3; Figs. 4.14a-c; Table 4.20). Dimensionless swing durations do not differ significantly among the three sampled ages in Infant 4 (Figs. 4.14d; Table 4.21).

When Infants 1-3 are combined, Group 1 individuals have significantly larger dimensionless stance durations than Group 2 (Fig. 4.15; Table 4.17). Group 1 individuals have significantly longer dimensionless swing durations than Group 2 individuals (Fig. 4.16; Table 4.17).

These results partially support the model predictions from Chapter 3. When limb mass is most distal in the infant baboons (Group 1), their dimensionless swing durations are all significantly longer. These long swing durations lead to relatively long stance durations in Infants 2 and 3. Infant 1 does not follow the prediction that long swing durations are met by long stance durations.

Spatial variables

Dimensionless stride length

The results for dimensionless stride lengths closely follow expectations derived from the results of dimensionless stride frequencies. In all three individuals that are divided into two age groups, dimensionless stride lengths are longer in Group 1 compared to Group 2 after dimensionless velocity has been taken into account (Figs. 4.17a-c; Table 4.22). Dimensionless stride lengths generally do not differ significantly within the

groups (Tables 4.23-4.25). There are some minor significant differences within groups, but these differences are much smaller than the between group differences.

In Infant 4, dimensionless stride lengths do not differ among the different age categories after dimensionless velocity has been taken into account (Figure 4.17d; Table 4.26). When Infants 1-3 are grouped together, Group 1 individuals have significantly longer dimensionless stride lengths compared to Group 2 individuals (Fig. 4.18; Table 4.17).

Hindlimb step length

Dimensionless step length is not correlated with dimensionless velocity for either Group 1 or Group 2 in Infant 1 (Table 4.27) and dimensionless step lengths do not differ significantly between the two groups (Table 4.27). There is no correlation between dimensionless step length and dimensionless velocity in either group in Infant 2 (Table 4.27) and dimensionless step lengths are significantly longer in Group 1 compared to Group 2 (Table 4.27). Dimensionless step length is not correlated with dimensionless velocity in Infant 3 (Table 4.27), and dimensionless step lengths are significantly longer in Group 1 compared to Group 2. In Infant 4, dimensionless step length is not significantly correlated with dimensionless velocity in Groups 1 and 3, and is significantly larger at its oldest age (Table 4.28). When Infants 1-3 are grouped together, Group 1 individuals use significantly longer dimensionless step lengths compared with Group 2 individuals (Table 4.17).

These results also support the model predictions from Chapter 3 regarding the connection between stance duration and step length. Infant 1 does not differ in

dimensionless step lengths or dimensionless stance durations between groups. Since the model predicts that relatively long steps and relatively long stance durations are linked, these results support the model. In Infants 2 and 3, both dimensionless step lengths and dimensionless stance durations are longer in Group 1 compared to Group 2, also supporting the model.

Hindlimb joint angles

Hindlimb angle at touchdown is correlated with dimensionless velocity in only Group 2 for Infant 1 and does not significantly differ between the two groups (Table 4.29). Hindlimb angle at lift-off is correlated with dimensionless velocity in only Group 2 for Infant 1 and does not significantly differ between the two groups (Table 4.30). Hindlimb angular excursion is not correlated with dimensionless velocity in either group for Infant 1 and is significantly larger in Group 2 (Table 4.31).

Hindlimb angle at touchdown is not correlated with dimensionless velocity in either group of Infant 2 (Table 4.29) and is significantly larger in Group 1 for this individual (Table 4.29). Hindlimb angle at lift-off is not correlated with dimensionless velocity in either group and is significantly larger in Group 2 for Infant 2 (Table 4.30). These differences between the two groups in hindlimb angle at touchdown and toe-off negate each other and total hindlimb excursion does not differ significantly between the two groups (Table 4.31) for Infant 2.

Hindlimb angle at touchdown is not correlated with dimensionless velocity in Infant 3 and does not differ significantly between the two groups (Table 4.29). Hindlimb angle at lift-off is not significantly correlated with dimensionless velocity in Infant 3 and

does not differ significantly between the two groups (Table 4.30). Total hindlimb excursion is not correlated with dimensionless velocity in this individual and does not differ significantly between the two groups (Table 4.31).

Hindlimb angle at touchdown is correlated with dimensionless velocity in Group 3 for Infant 4, but not for the other groups, and does not differ significantly between the three groups for this individual (Table 4.32). Hindlimb angle at lift-off is significantly correlated with dimensionless velocity in two groups for this individual (Table 4.33) but does not differ significantly among the three groups (Table 4.33). Hindlimb excursion is not correlated with dimensionless velocity at any age and is significantly larger at this infant's oldest age (Group 3) compared to each younger age (Table 4.34).

The effects of limb mass distribution changes on hindlimb angular excursions are difficult to interpret. Hindlimb excursions should be directly related to step length (see Chapter 3). Superficially, the results presented above do not support a link between the relatively longer strides and steps of individuals at young ages and their hindlimb angular excursions. There are two caveats to the results presented above that may influence interpretations. First, hindlimb angular excursion is directly related to step length if it is the hindlimb segment is defined by the hip marker and the point of the foot's ground contact. In digitigrade baboons, ground contact is the head of the metatarsals, but markers could not be placed on this joint in the present study. The use of the ankle marker to define the distal end of the hindlimb segment certainly affects the calculation of hindlimb angular excursion and therefore decreases the meaning of the results presented above.

It is also important to note that in the two individuals who used longer dimensionless steps in Group 1 (Infants 2 and 3), their mean hindlimb angular excursions are larger at younger ages. Their trend may be to have larger hindlimb excursion angles, despite the fact that this difference is not significant. The confidence limits for mean hindlimb angular excursions are much larger in Group 1 individuals for Infants 2 and 3 compared to Group 2. This difference could also have an impact on the results. If there is more variation in Group 1 individuals, then the significance of larger mean Group 1 hindlimb angles would be reduced.

Comparison with other mammals

Raw stride frequencies at the trot-gallop transition for a sample of adult primates and non-primate mammals (data from Alexander and Maloiy, 1984) were compared to predicted stride frequencies at the predicted trot-gallop transition velocities for this sample of infant baboons (Fig. 4.19). Predicted raw stride frequencies for the infant baboon sample at this physiologically equivalent velocity generally fall below the regression line for both adult primate and non-primate quadrupeds. The infant baboons use lower raw stride frequencies for their size at the trot-gallop transition compared to both adult primates and non-primate mammals. Note also that the adult primates use lower raw stride frequencies at the trot-gallop transition compared to non-primate quadrupeds (Fig. 4.19).

Dimensionless stride lengths for the infant baboons were compared with those of non-primate and primate quadrupeds (data from Alexander and Jayes, 1983; Alexander and Maloiy, 1983). At low dimensionless velocities, the infant baboons use longer

dimensionless stride lengths than adult primates, non-cursorial non-primates, and cursorial non-primates (Fig. 4.20). At higher dimensionless velocities, the infant baboons appear to converge upon the dimensionless stride lengths of the primate sample and even fall into the range of non-primate, non-cursorial mammals.

This result may be due to the decrease in swing phase duration with increasing velocity in this sample of infant baboons (see Table 4.8). From Chapter 3, it is evident that a reduction in swing phase duration with increasing velocity should lower the rate at which stride length increases with increasing velocity (see Chapter 3, Fig. 3.14). If the other non-primate quadrupeds in this sample maintain a constant swing duration at all velocities (as indicated for some taxa in the literature), then the reduction in swing duration with increasing velocity in the infant baboon sample should create a convergence of dimensionless stride lengths at high velocities (due to a lower rate of increase in dimensionless stride length in the infant baboons). There is no information about the change in swing duration with velocity in the literature used for these comparisons, so this possibility remains to be tested.

DISCUSSION

Impacts of limb mass distribution on kinematics

The hypothesis that limb mass distribution patterns have a significant impact on locomotor kinematics is supported by the results from this study. Although changes in kinematics with increasingly proximal limb mass concentrations are slight, they are consistent with predictions made from the hypothesized relationship between limb mass

distribution and locomotor kinematics (see Chapter 3). When the infant baboons have more distal limb mass concentrations, their dimensionless stride frequencies are lower and their dimensionless stride lengths are longer compared to older ages, when their limb mass is more proximally concentrated.

Importantly, Infant 4 serves as a control against an argument that these changes could be related to ontogenetic changes in neuro-muscular control mechanisms. Infant 4 did not show any change in functional limb inertial properties and did not undergo any change in spatio-temporal kinematics. If the changes in kinematics in Infants 1-3 were simply a result of ontogenetic changes in neuro-muscular control, then these same changes should have occurred in Infant 4 despite her lack of change in functional limb inertial properties.

Observed changes in stride frequency and stride length during ontogeny appear to be the result of changes in stance and swing durations. As the locomotor model predicted, because swing durations were relatively long in these individuals at young ages, stance durations were also generally long. These relatively long swing and stance durations led directly to the relatively low stride frequencies and long strides and steps used by these individuals. Step lengths and hindlimb angular excursions were not correlated with velocity because stance durations generally decreased in proportion to velocity^{-1}.

The data from this sample of infant baboons, provides a convincing explanation for the influence of limb mass distribution on locomotor variables. In an individual who has relatively distal limb mass concentrations, that distal limb mass will lead to relatively long swing durations. Relatively long swing durations necessitate relatively long stance

durations. Combined, these increased swing and stance durations lead to relatively low stride frequencies, long strides, and long steps.

As described earlier, the link between long dimensionless steps and long hindlimb angular excursions is not significant, but there does appear to be a trend in Infants 2 and 3. Had the hindlimb segment used in angular excursion calculation been measured from the hip to the point of ground contact, it seems reasonable to assume that these values would have been larger in Group 1 individuals when dimensionless steps were longer. In fact, it would not be possible for these results to differ, had hindlimb angular excursions been measured precisely (see Chapter 3). Given the results presented here though, it is not possible to strongly conclude that longer hindlimb angular excursions are the result of relatively distal limb mass concentrations, although this result deserves further analysis.

Comparison with ontogeny of vervet monkeys (*Cercopithecus aethiops*)

The only comparable ontogenetic data to this study for primates is from a combined longitudinal and cross sectional sample of vervet monkeys from Vilensky et al. (1988, 1990). Their results show mixed agreement with the results of the present study. It is important to note that vervet monkeys may not undergo the same amount of change in limb mass distribution during ontogeny as seen in the infant baboons. In Chapter 2, it was shown that rhesus monkeys undergo a smaller ontogenetic change due to their more arboreal locomotor preferences and the need to retain stronger grasping abilities in their hands and feet compared to the more terrestrial baboons. The same logic would be true for vervets, who are more arboreal than baboons (Fleagle, 1998).

Stance durations in the vervets decrease in proportion to velocity$^{-0.9}$, which is very close to the relationship seen in the baboon sample (Vilensky et al., 1988). This slope plus two standard deviations is equal to -1 (Vilensky et al., 1988). Vilensky et al. (1988) reported that swing durations generally increased with increasing body mass. It is important to note, however, that this increase is not significant. The standard deviations of mean swing durations overlap at all ages (Vilensky et al., 1988).

In geometrically similar animals, swing durations should increase with increasing size (see Myers and Steudel, 1997). If infant vervets have relatively more distally distributed limb mass at young ages, then their swing durations should be relatively long as well, weakening, or eliminating any increase in swing duration with increasing body size. Since Vilensky et al.'s (1988) vervets do not show significant increases in swing durations with increasing age and size, it is likely that these results match those of the infant baboons. The fact that the change in swing duration is either slight, or non-existent supports the contention that limb mass distribution changes during ontogeny may be influencing temporal kinematics in these vervets.

It would be expected, therefore, that stride frequencies would be relatively low in the younger aged vervets, since their swing durations appear to be relatively long. In both their cross sectional and longitudinal samples, Vilensky et al. (1988, 1990) found that stride duration (stride frequency^{-1}) at the trot-gallop transition (Vilensky et al., 1988,1990 refer to this as the run-gallop transition) did not vary in a systematic way with body mass. These data are consistent with the interpretation that stride frequencies at physiologically equivalent velocities should have a weak or non-existent relationship

with body mass during primate ontogeny, matching the results of the infant baboon sample.

Vilensky et al. (1988) tested the cross sectional group for dynamic similarity of stride lengths using the methods of Alexander and Jayes (1983). They report that their individuals walked with dynamically similar stride lengths across all Froude numbers (Vilensky et al., 1988). Unfortunately, they do not show the individuals separately, so it is not possible to determine whether residuals to their trend line differ with age, although the fit is very good. It is therefore difficult to interpret the relative stride length results reported by Vilensky et al. (1988) within the context of the results from this study.

Comparisons with other mammals

The results from Chapter 2 showed that the infant baboons have relatively more distal limb mass concentrations than other adult primates during much of their development, and have more distal limb mass concentrations than those of non-primate cursorial and non-cursorial quadrupeds. The results from this study show that the infant baboons also use lower stride frequencies than other adult primates and non-primate mammals. Although these results may not be as robust as the intra-individual results, due to the use of predicted values for the infant trot-gallop transition velocities, they are consistent with the hypothesis that distal limb mass distributions in the infants compared to those of adult mammals will result in reduced stride frequencies.

Infant baboons generally use longer dimensionless stride lengths compared to both adult primate and non-primate quadrupeds over most of their velocity range. This result is consistent with their more distal limb mass concentrations compared to most

adult primate and non-primate mammals (see Chapter 2). The convergence of the infant baboon dimensionless stride lengths with those of adult primates at higher velocities may be the result of a reduction in swing durations with increasing velocity in the infant baboon. This possibility highlights the complexity of inter-specific comparisons when the relationships between key locomotor variables and velocity may differ among mammalian taxa.

Despite these complications, kinematic differences between the infant baboons and other quadrupedal primate and non-primate mammals are consistent with their relatively more distally distributed limb mass.

Broad comparative evidence

The results from this study also have support from studies testing the dynamic similarity hypothesis in mammalian quadrupeds (see Alexander and Jayes, 1983; Alexander and Maloiy, 1984). If individuals depart from dynamic similarity in stride lengths, then individuals that use long dimensionless stride lengths should be those animals with the most distal limb mass concentrations. Non-cursorial quadrupeds use longer dimensionless strides at all dimensionless velocities compared to more cursorial quadrupeds (Alexander and Jayes, 1983). Additionally, as mentioned earlier, primates use longer relative stride lengths than both non-cursorial and cursorial quadrupedal mammals (Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1990).

Limb mass distribution differences among these broad groups may explain why they do not walk with dynamically similar stride lengths. Non-cursorial mammals appear to have more distal limb mass concentrations compared to their cursorial counterparts

(Myers and Steudel, 1997; Chapter 2), and they depart from dynamic similarity in a predictable way, with increases in dimensionless stride lengths. Primates also depart from overall dynamic similarity in the same way, and it seems likely that their longer dimensionless strides are related to their more distal concentrations of limb mass.

Although these broad comparisons support the hypothesized relationship between limb mass distribution and kinematics, deviations from these trends may also be informative. For example, the two data points for the domestic cats in Figure 3 of Alexander and Jayes (1983) show extremely long strides compared to the other cursorial mammals. In fact, both points lie above the regression line for non-cursorial quadrupeds (see Fig. 3 of Alexander and Jayes, 1983). This departure from dynamic similarity within the cursorial group provides further support for the results from the infant baboon sample. Cats have limb mass distributions that resemble those of non-cursorial quadrupeds more than cursors (Taylor et al., 1974; Chapter 2). Their long dimensionless strides compared to other more cursorial mammals are therefore consistent with their relatively distal limb mass concentrations.

In Alexander and Maloiy's (1984) examination of dynamic similarity in primate quadrupeds, the two points for *Papio* fall well below the regression line describing the relationship between dimensionless stride length and Froude number for primates in general (see their Fig. 2). Again, these deviations from within group dynamic similarity may be consistent with the results from this study. *Papio* has the most proximal limb mass concentrations of the primates that have been analyzed (see chapter 2; Raichlen, 2004).

So, this comparative evidence, along with the results from the present ontogenetic "natural experiment" strongly suggest that spatio-temporal kinematics must, in part, be driven by limb mass distribution patterns. This suggestion has important implications for the evolution of locomotor systems in both primate and non-primate quadrupeds.

Implications for the evolution of primate quadrupedalism

Several researchers have suggested that primates' unique quadrupedal kinematic characteristics evolved to facilitate locomotion in a small branch niche (Demes et al., 1990; Schmitt, 1999; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002; Schmitt, 2003). For example, primates' large limb angular excursions would increase stride length and therefore allow primates to use lower stride frequencies at a given velocity, thereby reducing potentially dangerous branch oscillations. Increased stance durations are part of the compliant gait model of primate walking proposed by Schmitt (1999). Increased stance durations would both help to reduce branch sway, and help reduce substrate reaction forces to alleviate problems associated with the crouched postures used by arboreal primates.

If the results from the infant baboon sample are expanded to primates in general, then the increased distal limb mass concentrations of primates may, in part, lead to their long strides, low stride frequencies, and long contact times. The conclusions of this study are compatible with the small branch niche hypothesis. In fact, this analysis provides a plausible explanation for how all these features of gait may have evolved as a related functional complex within the small branch niche. Early primates who invaded this niche would have first developed clawless grasping hands and feet. The features of gait that

would be advantageous in this niche would have been a by-product of this original adaptation. Importantly, because most extant primates have retained clawless grasping hands and feet for climbing or food manipulation, and therefore relatively distal limb mass concentrations compared to non-primates, the results from this study help explain why primates use these kinematic characteristics even when they no longer occupy a small branch niche.

Although the results from the infant baboons do not completely explain the large limb angular excursions of primates in terms of limb mass distribution patterns, as noted earlier, if primates use long steps, they must have large limb angular excursions. Since the long steps would be related to limb mass distributions, the large angular excursions would also be related to limb mass distributions. The spurious results from the infant baboon sample are likely due to methodology problems.

These results also do not preclude changes in kinematics that vary with substrate use, often used as a test of the small branch niche hypothesis (see Schmitt, 2003). Schmitt (2003) showed that several cercopithecoids increased forelimb protraction angles on arboreal compared to terrestrial substrates. Increased forelimb protraction angles should be associated with increased stride lengths (Larson et al., 2000). Based on the model described in Chapter 3 (eqs. 3.1 & 3.2), this increased protraction would likely be the result of increases in stance durations (increases in stance duration cause increases in step length which must be brought about by larger limb angular excursions). As noted in Chapter 3, relatively long stance durations are likely a response to increases in swing durations.

There is a possible reason to expect increased swing durations on arboreal substrates. When walking on a branch, a primate may maintain a relatively more extended knee and elbow during swing phase compared to terrestrial walking because its hands and feet no longer need to clear the substrate (see Schmitt et al., 1994 for an example of vervet monkeys passing their hands below the substrate during arboreal quadrupedalism). This more extended knee and elbow would increase each limbs' NPP relative to terrestrial locomotion (see Myers and Steudel, 1997; Raichlen, 2004), and therefore increase swing duration. The effect of this increased swing duration would be increased stance duration. As noted in Chapter 3, increased stance durations lead to longer steps which must be brought about by increases in limb angular excursions.

The unique kinematics of primate quadrupedalism may therefore be the result of primates lying at one end of a continuum of locomotor characteristics that encompasses all mammals. This continuum would match the continuum of limb inertial properties found in all mammals, and does not preclude non-primates from converging on primate locomotor characteristics.

Other mammals have been shown to share many of the primate kinematic characteristics described above (see Schmitt and Lemelin, 2002). In addition to walking with DSDC footfall sequences and higher hindlimb than forelimb vertical substrate reaction forces (Schmitt and Lemelin, 2002), Larson et al. (2000; 2001) showed that the woolly opossum (*Caluromys philander*) walks with large limb angular excursions, similar to those of primates (see also Schmitt and Lemelin, 2002). *Caluromys* also possesses grasping hands and feet (Lemelin, 1996; 1999) and Grand (1983; see also Chapter 2) showed that *Caluromys* does in fact have relatively distal limb mass

concentrations. Although no data are available showing relatively long strides and low stride frequencies in this taxon, if their large limb angular excursions are an indicator of these kinematic characteristics then they may also be the by-product of adaptations for grasping extremities.

Implications for mammalian quadrupedalism

The fact that intra-individual variability in stride length and stride frequency may be attributable to changes in limb mass distribution has implications for mammalian quadrupedalism in general. The results from this study provide an explanation for the variability in mammalian spatio-temporal kinematics that are not completely explained by body size.

The many studies that have examined mammalian locomotion tend to focus on taxa that differ widely in body size (e.g. Heglund and Taylor, 1974). The results from this study suggest that smaller differences in size, coupled with differences in limb mass distribution, may violate some of the general trends previously reported for mammalian locomotion (see Heglund and Taylor, 1974; McMahon, 1975; Heglund and Taylor, 1988). Specifically, the decrease in stride frequency at the trot-gallop transition with increasing body mass may not be true for individuals that are more similar in body mass but that differ in their limb inertial properties.

SUMMARY

The stride lengths and stride frequencies of infant baboons are dependent on their limb mass distribution patterns. As infant baboons age, and their limb mass becomes

more proximally concentrated, they use significantly higher dimensionless stride frequencies and significantly shorter dimensionless strides. Changes in stride lengths and stride frequencies that occur with limb mass distribution changes are brought about by changes in both swing and stance durations.

The connection between limb mass distribution and spatio-temporal kinematics has now been supported by four separate lines of evidence. First, in experiments where the limbs of both humans and dogs are loaded (increasing limb NPPs), swing durations and stride durations increase (see Inman et al., 1981; Martin, 1985; Holt et al., 1990; Skinner and Barrack, 1990; Steudel, 1990; Mattes et al., 2000). Second, the model proposed in Chapter 3 predicts these differences. Third, ontogenetic evidence strongly supports the connection between limb mass distribution and kinematics. And finally, comparative evidence supports this connection.

The relationship between limb mass distribution and locomotor kinematics may have important implications for the evolution of primate quadrupedalism. Primates in general have more distal limb mass than do most other mammals and this distal limb mass may explain their relatively long strides, low stride frequencies, large limb angular excursions, and increased stance durations compared to other mammalian quadrupeds.

The results from this study also suggest that individual differences in limb mass distributions may have important impacts on mammalian inter-specific variability in spatio-temporal kinematics. Much of our broad understanding of comparative mammalian quadrupedal biomechanics comes from studies that include few taxa that cover wide ranges of body mass. Future research into mammalian quadrupedalism

should include samples that are more similar in body mass yet differ in limb mass distribution patterns.

TABLES

Table 4.1. Description of sample and number of trials analyzed at each age.

Subject (SFBR ID)	Age (months)	Sex	n
Infant 1 (17194)	3.33	m	9
Infant 1 (17194)	4.27	m	10
Infant 1 (17194)	4.73	m	10
Infant 1 (17194)	5.87	m	16
Infant 1 (17194)	6.10	m	32
Infant 1 (17194)	7.50	m	26
Infant 2 (18573)	2.83	f	21
Infant 2 (18573)	3.67	f	19
Infant 2 (18573)	4.67	f	38
Infant 2 (18573)	4.97	f	31
Infant 2 (18573)	5.53	f	18
Infant 2 (18573)	7.40	f	13
Infant 2 (18573)	8.10	f	22
Infant 3 (18572)	<4.7	f	5
Infant 3 (18572)	4.70	f	20
Infant 3 (18572)	5.00	f	11
Infant 3 (18572)	5.57	f	12
Infant 3 (18572)	6.23	f	23
Infant 3 (18572)	7.43	f	33
Infant 3 (18572)	8.13	f	29
Infant 3 (18572)	8.97	f	69
Infant 4 (17220)	2.60	f	11
Infant 4 (17220)	4.47	f	8
Infant 4 (17220)	7.23	f	21

Note: Subject describes the infant number that will be used in the text, its SFBR identification number is listed in parentheses. n is the number of accepted trials analyzed and included here for each sampled age.

Table 4.2. Results of ANOCOVA comparing dimensionless hindlimb NPPs in Infant 1 at all sampled ages.

Age	4.27	4.73	5.98	7.50	LSmean	95% confidence limit
3.33	0.78	0.93	**<.0001**	**<.0001**	5.01	0.07
4.27	-	1.00	**<.0001**	**<.0001**	4.95	0.06
4.73		-	**<.0001**	**<.0001**	4.97	0.06
5.98			-	0.95	4.75	0.03
7.50				-	4.73	0.04

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.3. Results of ANOCOVA comparing dimensionless hindlimb NPPs in Infant 2 at all sampled ages.

Age	2.83	3.67	4.67	4.97	5.53	7.40	8.10	LSmean	95% confidence limit
2.03	0.61	0.08	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	5.20	0.09
2.83	-	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	5.30	0.07
3.67		-	**<.0001**	**<.0001**	**0.01**	**0.01**	**<.0001**	5.02	0.08
4.67			-	0.89	0.45	0.81	0.93	4.68	0.06
4.97				-	**0.05**	0.95	1.00	4.63	0.06
5.53					-	0.36	0.06	4.77	0.07
7.40						-	0.11	4.48	0.25
8.10							-	4.62	0.07

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.4. Results of ANOCOVA comparing dimensionless hindlimb NPPs in Infant 3 at all sampled ages.

Age	4.17	4.70	5.00	5.57	6.23	7.43	8.13	8.97	LS mean	95% confidence interval
3.70	0.66	0.48	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	5.13	0.01
4.17	-	1.00	**0.005**	**0.01**	**<.0001**	**0.00**	**0.01**	**0.001**	4.79	0.01
4.70		-	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	4.79	0.01
5.00			-	1.00	0.96	1.00	1.00	1.00	4.47	0.01
5.57				-	0.68	1.00	1.00	1.00	4.47	0.01
6.23					-	0.72	0.98	0.36	4.47	0.005
7.43						-	1.00	1.00	4.47	0.004
8.13							-	1.00	4.47	0.01
8.97								-	4.47	0.003

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.5. Results of ANOCOVA comparing dimensionless hindlimb NPPs in Infant 4 at all sampled ages.

Age	4.47	7.23	LS mean	95% confidence interval
2.60	1.00	0.32	4.14	0.10
4.47	-	0.38	4.14	0.11
7.23		-	4.05	0.07

Note: Table lists p-values for the probability that LSmeans do not differ between each age. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.6. Comparisons of forelimb and hindlimb kinematics variables

Variable	LSmean	95% CI	H_0:LSmean1=LSmean2
Hindlimb Stride Frequency (s^{-1})	0.16	0.005	0.9991
Forelimb Stride Frequency (s^{-1})	0.16	0.005	
Hindlimb Stride Length (m)	-0.29	0.005	0.6825
Forelimb Stride Length (m)	-0.28	0.005	
Hindlimb Stance Duration (s)	-0.43	0.007	0.1391
Forelimb Stance Duration (s)	-0.42	0.007	
Hindlimb Swing Duration (s)	-0.51	0.006	0.1823
Forelimb Swing Duration (s)	-0.52	0.006	

Note: ANOCOVA applied to forelimb and hindlimb values of the same variables with velocity as the covariate. H_0 is the probability that LSmean1 (hindlimb LSmean) equals LSmean2 (forelimb LSmean).

Table 4.7. Least-squares regression statistics for the relationship between stance duration and velocity in the infant baboon sample.

Group	r^2	p	slope	95% CI slope	intercept	95% CI intercept
Infant 1 Group 1	0.958	<.0001	-1.008	0.083	-0.655	0.027
Infant 1 Group 2	0.969	<.0001	-1.052	0.044	-0.578	0.011
Infant 2 Group 1	0.964	<.0001	-1.030	0.067	-0.505	0.015
Infant 2 Group 2	0.953	<.0001	-1.097	0.044	-0.554	0.010
Infant 3 Group 1	0.972	<.0001	-1.121	0.082	-0.512	0.018
Infant 3 Group 2	0.915	<.0001	-1.058	0.048	-0.519	0.010
Infant 4 Group 1	0.919	<.0001	-0.906	0.202	-0.573	0.111
Infant 4Group 2	0.748	0.006	-0.723	0.420	-0.463	0.148
Infant 4 Group 3	0.798	<.0001	-0.969	0.234	-0.467	0.046

Note: r^2 is the correlation coefficient for stance duration vs. velocity, p is the probability that the slope is different from 0, and CI is the 95% confidence interval for the slope and intercept.

Table 4.8. Least-squares regression statistics for the relationship between swing duration and velocity in the infant baboon sample.

Grouping	r^2	p-value	slope	95% CI slope	intercept	95% CI intercept
Infant 1 Group 1	0.704	<.0001	-0.337	0.086	-0.557	0.028
Infant 1 Group 2	0.601	<.0001	-0.323	0.062	-0.581	0.016
Infant 2 Group 1	0.669	<.0001	-0.415	0.096	-0.566	0.023
Infant 2 Group 2	0.485	<.0001	-0.285	0.053	-0.557	0.012
Infant 3 Group 1	0.523	<.0001	-0.254	0.105	-0.532	0.027
Infant 3 Group 2	0.150	<.0001	-0.131	0.046	-0.523	0.010
Infant 4 Group 1	0.586	0.006	-0.477	0.302	-0.671	0.166
Infant 4Group 2	0.309	0.153	-0.520	0.777	-0.601	0.275
Infant 4 Group 3	0.486	0.0004	-0.412	0.203	-0.494	0.040

Note: R^2 is the correlation coefficient for stance duration vs. velocity. P is the probability that the slope is different from 0. CI is the 95% confidence interval for the slope and intercept.

Table 4.9. LSmeans and their 95% confidence limits for between group comparison of raw stride frequencies in Infants 1-3.

Grouping	LSmean	95% Confidence Limits	H_0:LSMean1=LSMean2
Infant 1 Group 1	0.19	0.01	**0.0028**
Infant 1 Group 2	0.17	0.01	
Infant 2 Group 1	0.18	0.01	**0.0074**
Infant 2 Group 2	0.20	0.01	
Infant 3 Group 1	0.13	0.02	0.1894
Infant 3 Group 2	0.14	0.01	

Note: LSmeans calculated after raw velocity was taken into account using ANCOVA. H_0 is the probability that LSmean1 (Group 1) is equal to LSmean2 (Group 2) for each individual. Significant differences are indicated by bold-faced type.

Table 4.10. LSmeans and 95% confidence limits, and significance values for between group comparison of raw stride frequencies in Infant 4.

Group	2	3	LS mean	95% confidence limits
1	0.17	**<.0001**	0.12	0.05
2	-	0.07	0.05	0.06
3		-	-0.02	0.03

Note: Table lists p-values for the probability that LSmeans are equal among ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.11. Least-squares regression statistics for stride frequencies vs. velocity for all individuals at all ages.

Age	Body Mass	Intercept	Intercept 95% CI	Slope	Slope 95% CI	p
Infant 1						
3.33	1.30	0.30	0.01	0.66	0.04	<.0001
4.27	1.53	0.29	0.03	0.69	0.14	<.0001
4.73	1.79	0.28	0.08	0.67	0.21	<.0001
5.98	2.38	0.26	0.01	0.65	0.04	<.0001
7.50	2.44	0.27	0.02	0.75	0.07	<.0001
Infant 2						
4.70	1.82	0.20	0.01	0.68	0.05	<.0001
5.00	2.08	0.24	0.03	0.51	0.09	<.0001
5.57	1.98	0.21	0.04	0.55	0.14	<.0001
6.23	2.39	0.20	0.01	0.55	0.05	<.0001
7.43	2.76	0.22	0.01	0.68	0.08	<.0001
8.13	2.95	0.22	0.04	0.69	0.18	<.0001
8.97	2.74	0.20	0.01	0.60	0.05	<.0001
Infant 3						
2.03	1.02	0.22	0.02	0.70	0.07	<.0001
2.83	1.50	0.23	0.02	0.76	0.07	<.0001
3.67	1.67	0.29	0.03	0.74	0.08	<.0001
4.67	1.66	0.26	0.01	0.71	0.05	<.0001
4.97	1.99	0.27	0.01	0.70	0.07	<.0001
5.53	1.99	0.24	0.02	0.70	0.10	<.0001
7.40	2.78	0.19	0.04	0.55	0.19	<.0001
8.10	2.66	0.19	0.02	0.56	0.07	<.0001
Infant 4						
2.60	1.14	0.33	0.09	0.77	0.16	<.0001
4.47	1.81	0.23	0.15	0.64	0.43	0.01
7.23	2.73	0.17	0.03	0.72	0.15	<.0001

Note: All regression statistics were calculated on log transformed date. p is the probability that the slope is equal to 0.

Table 4.12. LSMeans and 95% confidence limits for between group comparisons of dimensionless stride frequency in Infants 1-3

Group	LSMean	95% Confidence Limits	H_0:LSMean1=LSMean2
Infant 1 Group 1	-0.610	0.011	<.0001
Infant 1 Group 2	-0.561	0.007	
Infant 2 Group 1	-0.606	0.012	<.0001
Infant 2 Group 2	-0.540	0.007	
Infant 3 Group 1	-0.662	0.016	<.0001
Infant 3 Group 2	-0.591	0.005	

Note: LSMean and 95% confidence limits were calculated from ANCOVAs with dimensionless velocity as the covariate. H_0 is the probability that LSMean1 (Group 1) is equal to LSMean2 (Group 2).

Table 4.13. LSMeans and 95% confidence limits for comparisons of dimensionless stride frequency among all ages for Infant 1.

Group	Age	4.267	4.733	5.983	7.500	LS mean	95% CI
1	3.333	0.944	0.997	**0.001**	**0.001**	-0.619	0.022
1	4.267		1.000	**0.032**	**0.028**	-0.607	0.025
1	4.733			0.696	0.651	-0.608	0.061
2	5.983				0.998	-0.567	0.010
2	7.500					-0.565	0.013

Note: Table lists p-values for the probability that LSmeans are equal among the sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.14. LSMeans and 95% confidence limits for comparisons of dimensionless stride frequency among all ages for Infant 2.

Group	Age	3.67	4.67	4.97	5.53	7.40	8.10	LS mean	95% CI
1	2.83	0.135	**<.0001**	**<.0001**	**<.0001**	**0.024**	**<.0001**	-0.614	0.015
1	3.67		**<.0001**	**<.0001**	**<.0001**	0.152	**0.003**	-0.597	0.016
2	4.67			**0.001**	0.984	0.232	**0.044**	-0.545	0.012
2	4.97				**0.003**	**0.006**	**<.0001**	-0.514	0.012
2	5.53					0.244	0.074	-0.545	0.016
2	7.40						0.842	-0.568	0.036
2	8.10							-0.564	0.014

Note: Table lists p-values for the probability that LSmeans are equal among the sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.15. LSMeans and 95% confidence limits for comparisons of dimensionless stride frequency among all ages for Infant 3.

Group	Age	5.00	5.57	6.23	7.43	8.13	8.97	LS mean	95% CI
1	≤4.7	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	-0.662	0.015
2	5.00	-	0.998	0.945	0.930	1.000	0.999	-0.590	0.021
2	5.57		-	0.999	0.542	0.986	1.000	-0.598	0.020
2	6.23			-	0.080	0.891	0.966	-0.603	0.015
2	7.43				-	0.999	0.109	-0.577	0.011
2	8.13					-	0.988	-0.584	0.027
2	8.97						-	-0.595	0.008

Note: Table lists p-values for the probability that LSmeans are equal among the sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.16. LSMeans and 95% confidence limits for comparisons of dimensionless stride frequency among all ages for Infant 4.

Group	Age	4.47	7.23	LS mean	95% CI
1	2.60	0.959	0.176	-0.699	0.045
2	4.47	-	0.425	-0.708	0.055
3	7.23		-	-0.746	0.027

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.17. LSMeans and 95% confidence limits for between group comparisons of kinematic variables in combined sample (Infants 1-3).

Variable	LSmean1	CI	LSmean2	CI	H_0:LSMean1=LSMean2
Dimensionless Stride Frequency	-0.632	0.008	-0.580	0.004	**<.0001**
Dimensionless Stride Length	0.277	0.008	0.223	0.004	**<.0001**
Dimensionless Stance Duration	0.358	0.012	0.312	0.006	**<.0001**
Dimensionless Swing Duration	0.284	0.012	0.220	0.006	**<.0001**
Dimensionless Step Length	-0.034	0.014	-0.062	0.007	**0.001**

Note: LSmean1 is the least squares mean for Group 1 for each variable after dimensionless velocity has been taken into account. LSmean2 is the least squares mean for Group 2 for each variable after dimensionless velocity has been taken into account. H_0 is the probability that LSmean1 is equal to LSmean2.

Table 4.18. LSMeans and 95% confidence limits for between group comparisons of dimensionless stance durations in each of the infant baboons.

Grouping	LSMean	95% confidence limit	H_0:LSMean1=LSMean2
Infant 1 Group 1	0.297	0.019	0.909
Infant 1 Group 2	0.298	0.011	
Infant 2 Group 1	0.349	0.016	**0.002**
Infant 2 Group 2	0.252	0.009	
Infant 3 Group 1	0.415	0.022	**<.0001**
Infant 3 Group 2	0.326	0.007	

Note: LSMean is the least squares mean dimensionless stance durations for each group after dimensionless velocity has been taken into account. H_0 is the probability that LSMean1 (Group 1) is equal to LSMean2.

Table 4.19. LSMeans and 95% confidence limits for between group comparisons of dimensionless stance durations in Infant 4.

Group	2	3	LS mean	95% CI
1	0.997	0.831	0.497	0.067
2	-	0.827	0.493	0.080
3		-	0.519	0.040

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.20. LSMeans and 95% confidence limits for between group comparisons of dimensionless swing durations in each of the infant baboons.

Grouping	LSMEAN	95% confidence limit	H_0:LSMean1=LSMean2
Infant 1 Group 1	0.283	0.022	**<.0001**
Infant 1 Group 2	0.201	0.014	
Infant 2 Group 1	0.261	0.020	**<.0001**
Infant 2 Group 2	0.202	0.011	
Infant 3 Group 1	0.299	0.026	**<.0001**
Infant 3 Group 2	0.226	0.009	

Note: LSMean is the least squares mean dimensionless stance durations for each group after dimensionless velocity has been taken into account. H_0 is the probability that LSMean1 (Group 1) is equal to LSMean2.

Table 4.21. LSMeans and 95% confidence limits for between group comparisons of dimensionless swing durations in Infant 4.

Group	2	3	LS mean	95% CI
1	0.798	0.096	0.266	0.068
2	-	0.513	0.299	0.082
3		-	0.350	0.041

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.22. LSMeans and 95% confidence limits for between group comparisons of dimensionless stride lengths in Infants 1-3.

Grouping	LSMEAN	95% confidence limit	H_0:LSMean1=LSMean2
Infant 1 Group 1	0.244	0.012	**<.0001**
Infant 1 Group 2	0.190	0.007	
Infant 2 Group 1	0.299	0.013	**<.0001**
Infant 2 Group 2	0.234	0.007	
Infant 3 Group 1	0.303	0.017	**<.0001**
Infant 3 Group 2	0.231	0.005	

Note: LSMean is the least squares mean dimensionless stance durations for each group after dimensionless velocity has been taken into account. H_0 is the probability that LSMean1 (Group 1) is equal to LSMean2.

Table 4.23. LSMeans and 95% confidence limits for comparisons of dimensionless stride length among all ages for Infant 1.

Group	Age	4.27	4.73	5.98	7.50	LS mean	95% CI
1	3.33	0.496	0.354	**0.001**	**0.001**	0.246	0.025
1	4.27	-	0.566	**0.023**	**0.013**	0.233	0.027
1	4.73		-	0.708	0.590	0.212	0.068
2	5.98			-	0.539	0.199	0.011
2	7.50				-	0.193	0.016

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.24. LSMeans and 95% confidence limits for comparisons of dimensionless stride length among all ages for Infant 2.

Group	Age	3.67	4.67	4.97	5.53	7.40	8.10	LS mean	95% CI
1	2.83	0.807	**<.0001**	**<.0001**	**<.0001**	0.161	**0.006**	0.307	0.016
1	3.67	-	**<.0001**	**<.0001**	**0.001**	0.595	0.321	0.290	0.017
2	4.67		-	0.167	0.999	0.973	**0.045**	0.234	0.013
2	4.97			-	0.119	0.409	**<.0001**	0.210	0.013
2	5.53				-	0.996	0.306	0.239	0.017
2	7.40					-	0.997	0.252	0.039
2	8.10						-	0.265	0.016

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.25. LSMeans and 95% confidence limits for comparisons of dimensionless stride length among all ages for Infant 3.

Group	Age	5.00	5.57	6.23	7.43	8.13	8.97	LS mean	95% CI
1	≤4.7	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	0.303	0.016
2	5.00		0.233	0.215	0.642	0.948	0.064	0.218	0.023
2	5.57			0.920	**0.047**	0.276	0.744	0.237	0.022
2	6.23				**0.023**	0.270	0.575	0.236	0.016
2	7.43					0.764	**0.0001**	0.212	0.012
2	8.13						0.122	0.217	0.029
2	8.97							0.241	0.009

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.26. LSMeans and 95% confidence limits for between group comparisons of dimensionless stride length in Infant 4.

Group	2	3	LS mean	95% confidence limits
1	0.941	0.213	0.191	0.042
2	-	0.495	0.201	0.050
3		-	0.233	0.026

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant.

Table 4.27. Means and 95% confidence limits for between group comparisons of dimensionless step lengths in Infants 1-3.

Grouping	r^2	p	Mean	95% CI	H_0:Mean1=LSMean2
Infant 1 Group 1	0.00002	0.983	-0.114	0.015	0.446
Infant 1 Group 2	0.016	0.284	-0.107	0.009	
Infant 2 Group 1	0.052	0.157	-0.074	0.016	<.0001
Infant 2 Group 2	0.00041	0.825	-0.088	0.009	
Infant 3 Group 1	0.045	0.309	-0.009	0.026	<.0001
Infant 3 Group 2	0.00003	0.938	-0.024	0.010	

Note: r^2 is correlation coefficient for the relationship between dimensionless step length and dimensionless velocity. p is the significance value for this correlation. Mean is the least squares mean dimensionless stance durations for each group after dimensionless velocity has been taken into account. H_0 is the probability that Mean1 (Group 1) is equal to Mean2.

Table 4.28. LSMeans and 95% confidence limits for between group comparisons of dimensionless step length in Infant 4.

Group	2	3	LS mean	95% CI	r^2	p
1	0.977	**0.029**	-0.065	0.039	0.090	0.369
2	-	**0.038**	-0.072	0.047	0.636	0.018
3		-	-0.005	0.023	0.043	0.369

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant. r^2 is correlation coefficient for the relationship between dimensionless step length and dimensionless velocity. p is the significance value for this correlation.

Table 4.29. LSMeans and 95% confidence limits for between group comparisons of hindlimb angle at touchdown in Infants 1-3.

Group	r^2	p-value	LSmean/ Mean	95% confidence limit	H_0:LSMean1=LSMean2
Infant 1 Group 1	0.018	0.489	16.594	3.125	0.323
Infant 1 Group 2	0.130	0.002	18.299	1.382	
Infant 2 Group 1	0.062	0.122	32.309	2.504	**0.0004**
Infant 2 Group 2	0.001	0.750	27.025	1.434	
Infant 3 Group 1	0.005	0.728	23.424	2.709	0.140
Infant 3 Group 2	0.013	0.132	21.251	1.018	

Note: r^2 is correlation coefficient for the relationship between hindlimb angle at touchdown and dimensionless velocity. p is the significance value for this correlation. LSMean is the least squares mean hindlimb touchdown angles for each group after dimensionless velocity has been taken into account. H_0 is the probability that LSMean1 (Group 1) is equal to LSMean2. Note that LSmeans were calculated for Infant 1 because of the significant correlation in Group 2, while means were compared for Infants 2 and 3 because correlations were not significant.

Table 4.30. LSMeans and 95% confidence limits for between group comparisons of hindlimb angle at lift-off in Infants 1-3.

Group	r^2	p-value	LSMEAN/ Mean	95% confidence limit	H_0:LSMean1=LSMean2
Infant 1 Group 1	0.059	0.205	-34.843	1.772	0.124
Infant 1 Group 2	0.156	0.001	-36.472	1.092	
Infant 2 Group 1	0.101	0.046	-29.507	2.091	**0.016**
Infant 2 Group 2	0.006	0.399	-32.435	1.099	
Infant 3 Group 1	0.003	0.787	-36.585	2.722	0.670
Infant 3 Group 2	0.002	0.573	-35.955	1.023	

Note: R^2 is correlation coefficient for the relationship between hindlimb angle at lift-off and dimensionless velocity. P is the significance value for this correlation. LSMean is the least squares mean hindlimb lift-off angles for each group after dimensionless velocity has been taken into account. H_0 is the probability that LSMean1 (Group 1) is equal to LSMean2. Note that LSmeans were calculated when for an individual if one group had a significant correlation.

Table 4.31. LSMeans and 95% confidence limits for between group comparisons of hindlimb angular excursion in Infants 1-3.

Group	r^2	p-value	LSMEAN	95% confidence limit	H_0:LSMean1=LSMean2
Infant 1 Group 1	0.006	0.679	49.178	1.957	**0.001**
Infant 1 Group 2	0.001	0.827	53.385	1.225	
Infant 2 Group 1	0.251	0.001	61.031	2.280	0.256
Infant 2 Group 2	0.010	0.273	59.516	1.305	
Infant 3 Group 1	0.010	0.639	60.009	3.161	0.103
Infant 3 Group 2	0.004	0.410	57.206	1.188	

Note: r^2 is correlation coefficient for the relationship between hindlimb angular excursion and dimensionless velocity. p is the significance value for this correlation. LSMean is the least squares mean hindlimb angular excursions for each group after dimensionless velocity has been taken into account. H_0 is the probability that LSMean1 (Group 1) is equal to LSMean2. Note that LSmeans were calculated when for an individual if one group had a significant correlation.

Table 4.32. LSMeans and 95% confidence limits for between group comparisons of hindlimb angle at touchdown in Infant 4.

Group	2	3	LS mean	95% confidence limits	r^2	p-value
1	0.970	0.100	18.224	6.984	0.115	0.309
2	-	0.579	19.890	12.481	0.035	0.658
3		-	26.266	3.245	0.280	**0.014**

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant. r^2 is correlation coefficient for the relationship between hindlimb angle at touchdown and dimensionless velocity. p is the significance value for this correlation.

Table 4.33. LSMeans and 95% confidence limits for between group comparisons of hindlimb angle at lift-off in Infant 4.

Group	2	3	LS mean	95% confidence limits	r^2	p-value
1	0.768	0.798	-35.246	6.187	0.044	0.536
2	-	0.921	-39.580	11.058	0.675	**0.012**
3		-	-37.401	2.875	0.303	**0.010**

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant. r^2 is correlation coefficient for the relationship between hindlimb angle at lift-off and dimensionless velocity. p is the significance value for this correlation.

Table 4.34. LSMeans and 95% confidence limits for between group comparisons of hindlimb angular excursion in Infant 4.

Group	2	3	LS mean	95% confidence limits	r^2	p-value
1	1.000	0.003	54.681	3.956	0.018	0.695
2	-	0.009	54.713	4.638	0.166	0.316
3		-	63.161	2.863	0.015	0.601

Note: Table lists p-values for the probability that LSmeans are equal among sampled ages. Also listed is the LSmean for each age, and its 95% confidence interval. Values in bold face are considered significant. r^2 is correlation coefficient for the relationship between hindlimb angular excursion and dimensionless velocity. p is the significance value for this correlation.

FIGURES

Figure 4.1. Experimental set-up.

Tunnel shown has two sections separated by approximately 3 feet. Five infra-red cameras are placed in an arc on one side of the tunnel. Reflective markers are attached to both sides of the individual prior to tunnel entry.

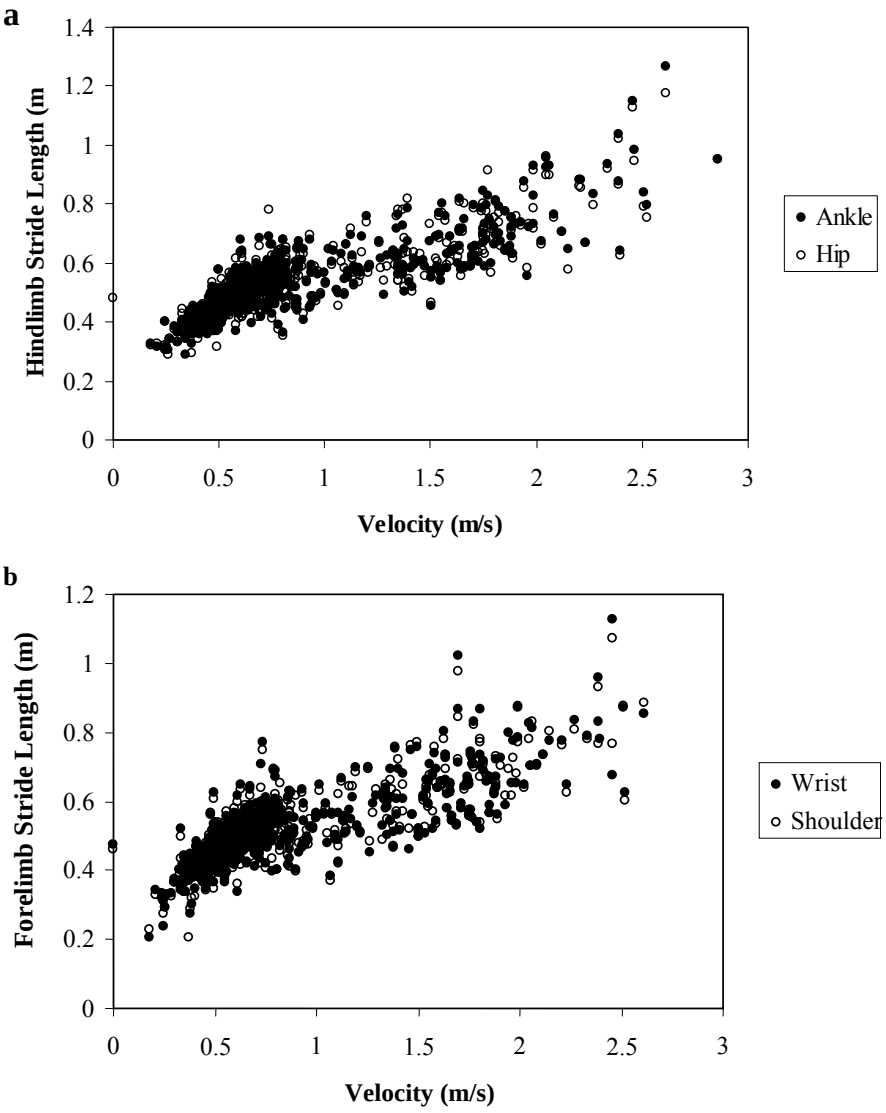


Figure 4.2. Comparison of stride lengths calculated using the a) ankle and hip markers and b) wrist and shoulder markers.

Stride lengths calculated using the hip markers do not significantly differ from those calculated using the ankle markers (ANCOVA p=.81). Stride lengths calculated using the wrist markers do not significantly differ from those calculated using the shoulder markers (ANCOVA p=.92).

Figure 4.3. Measurement of forelimb and hindlimb angles.

Hindlimb angle (a) is measured as the angle between the hindlimb (segment from hip marker to ankle marker) and a vertical line passing through the hip. Forelimb angle (b) is measures as the angle between the forelimb (segment from the shoulder marker to the wrist marker) and a vertical line passing through the shoulder.

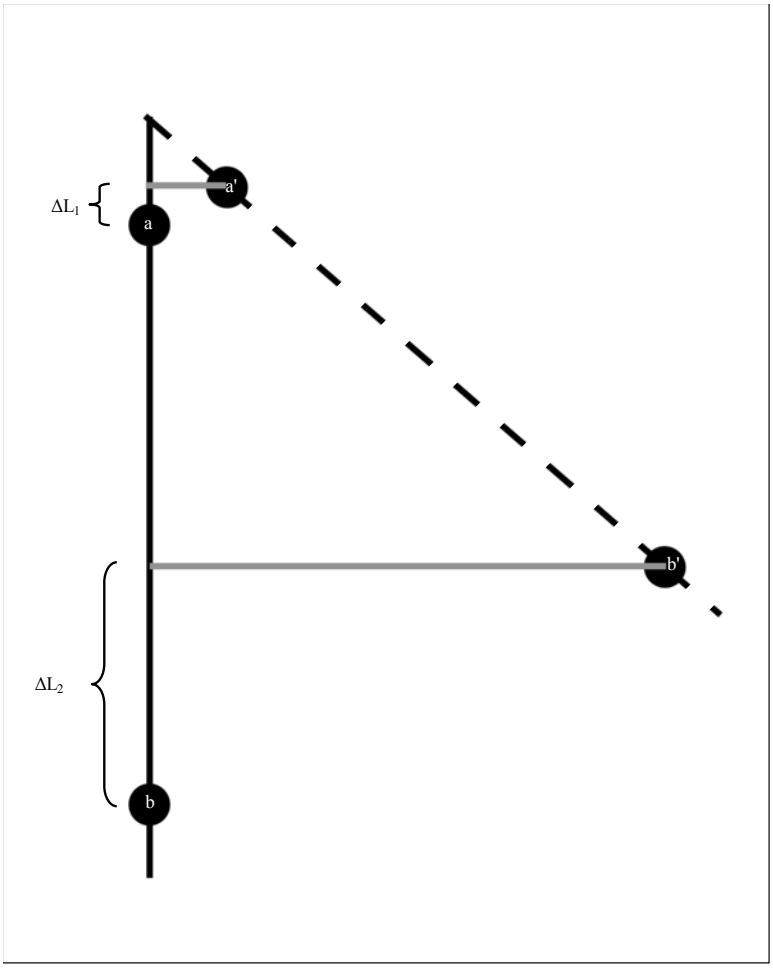


Figure 4.4. Schematic diagram of the effects of flexion on limb NPP.

Consider a distal limb segment (solid line) with its center of mass (a) very proximal. If the limb flexes (dashed line), then the vertical distance of the center of mass (a') becomes more proximal by L_1. If the segment's center of mass is more distal (b), then the same amount of flexion causes the distance of the center of mass to move proximally by a greater amount (L_2). $L_2 > L_1$. If this segment represented above were the forearm of a quadruped, then flexing the elbow would cause a greater shift in the whole limb center of mass in an individual whose forearm's center of mass was more distal (b), compared to a more proximal center of mass position (a).

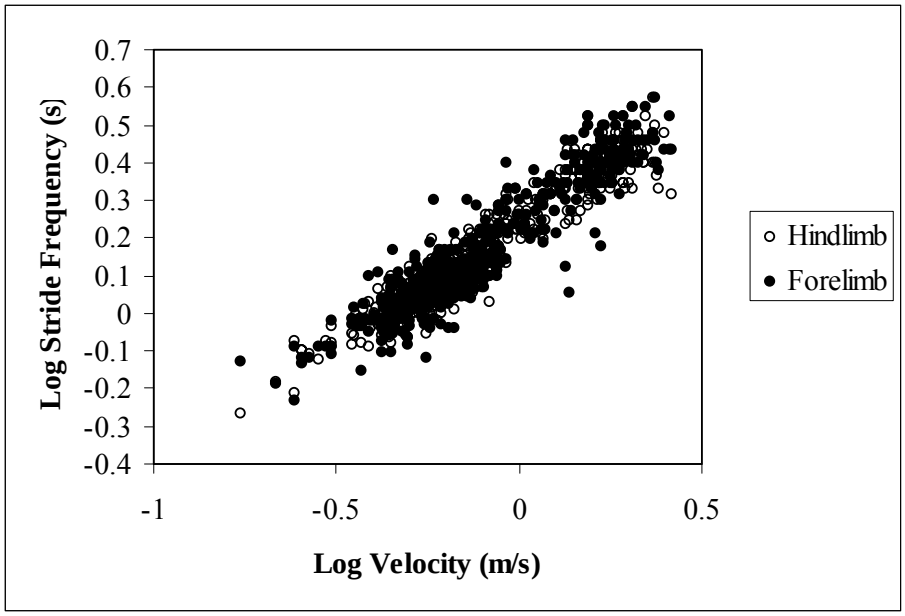


Figure 4.5. Comparison of forelimb and hindlimb stride frequencies in the combined sample of infant baboons.

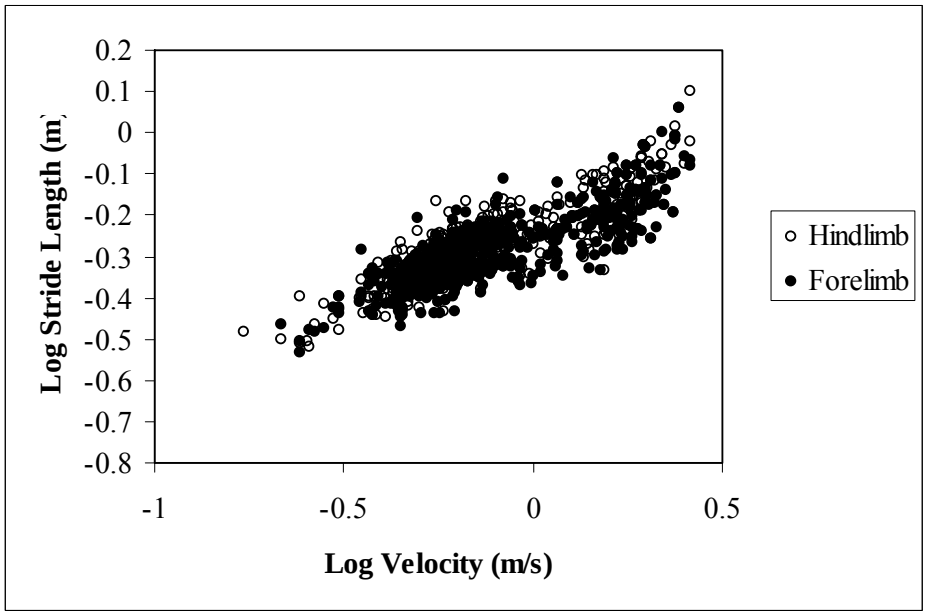


Figure 4.6. Comparison of forelimb and hindlimb stride lengths in the combined sample of infant baboons.

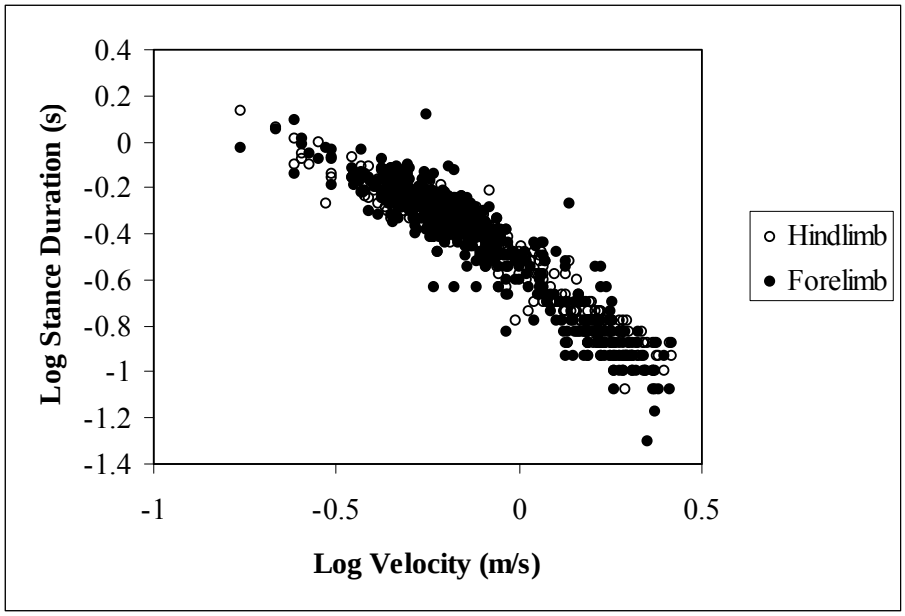


Figure 4.7. Comparison of forelimb and hindlimb stance durations in the combined sample of infant baboons.

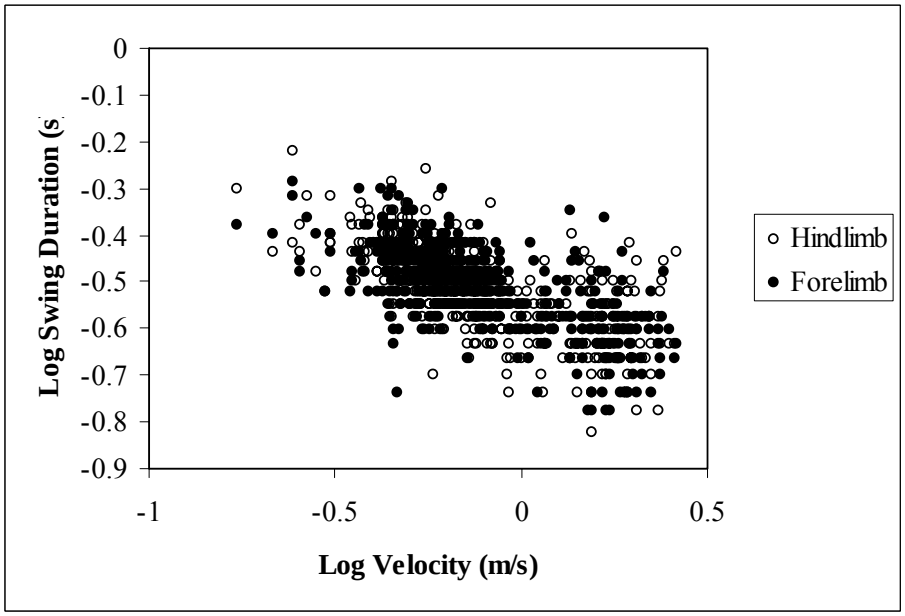


Figure 4.8. Comparison of forelimb and hindlimb swing durations in the combined sample of infant baboons.

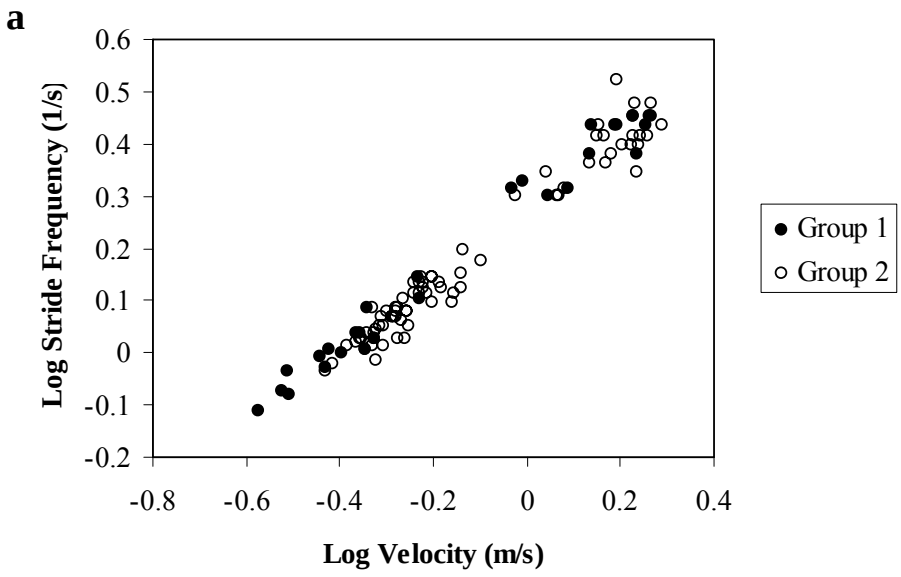


Figure 4.9a. Between group comparisons of raw stride frequencies over the entire raw velocity range for Infant 1.

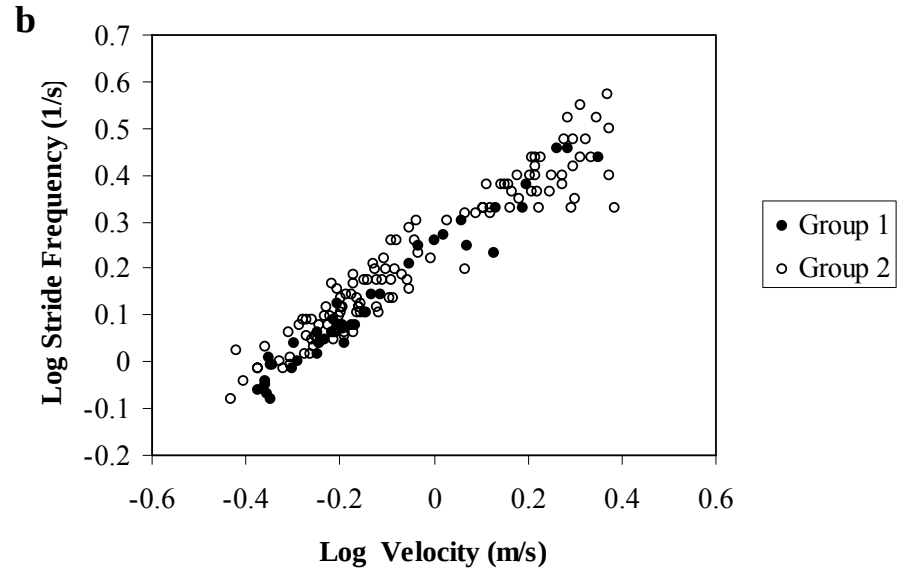


Figure 4.9b. Between group comparisons of raw stride frequencies over the entire raw velocity range for Infant 2.

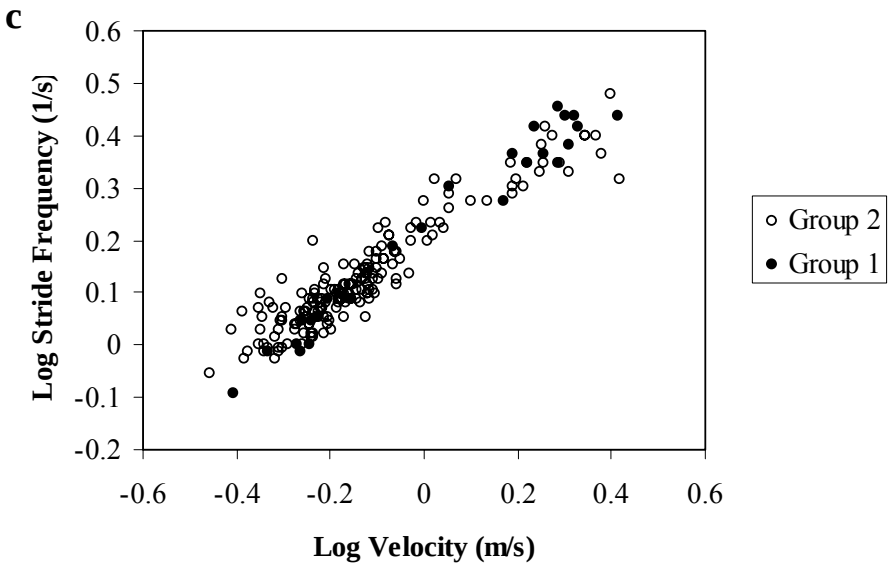
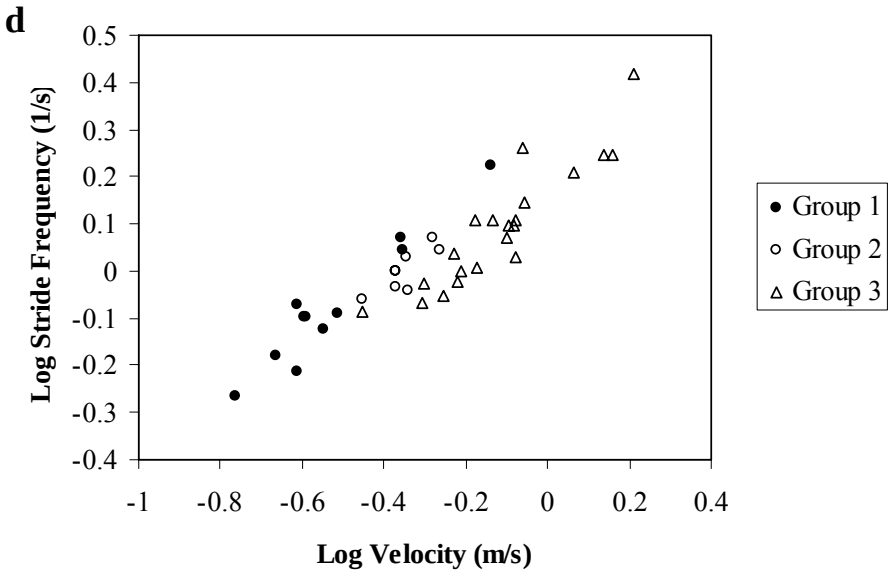


Figure 4.9c. Between group comparisons of raw stride frequencies over the entire raw velocity range for Infant 3.



Figures 4.9d. Between group comparisons of raw stride frequencies over the entire raw velocity range for Infant 4.

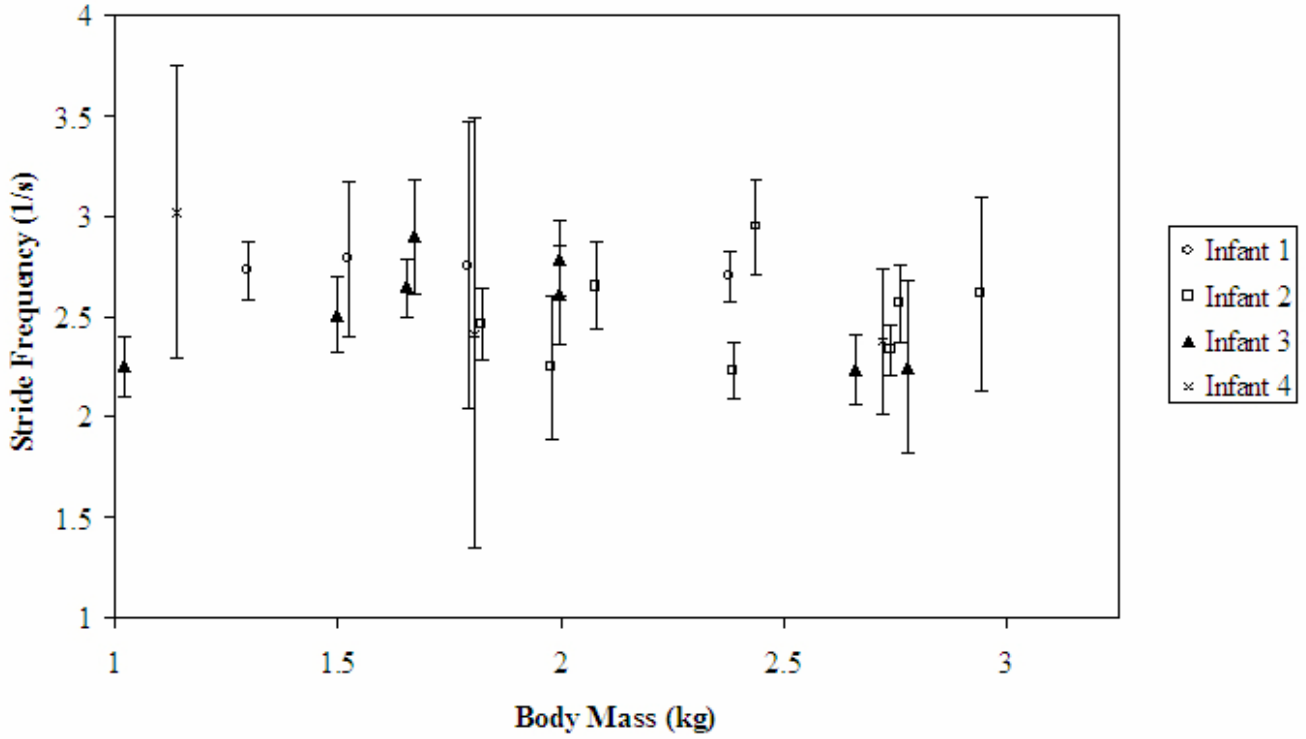


Figure 4.10. Stride frequencies at the trot-gallop transition for the entire infant baboon sample. Predicted stride frequencies at the predicted trot-gallop transition velocity for Infant 1 (open circles), Infant 2 (open squares), Infant 3 (closed triangles), Infant 4 (x), bars are 95% confidence intervals. See text for further details.

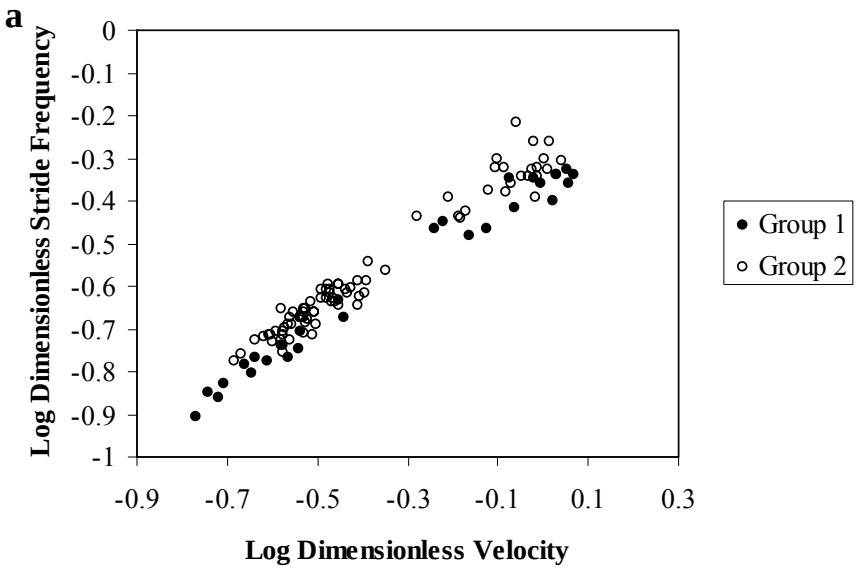


Figure 4.11a. Between group comparisons of dimensionless stride frequencies in Infant 1.

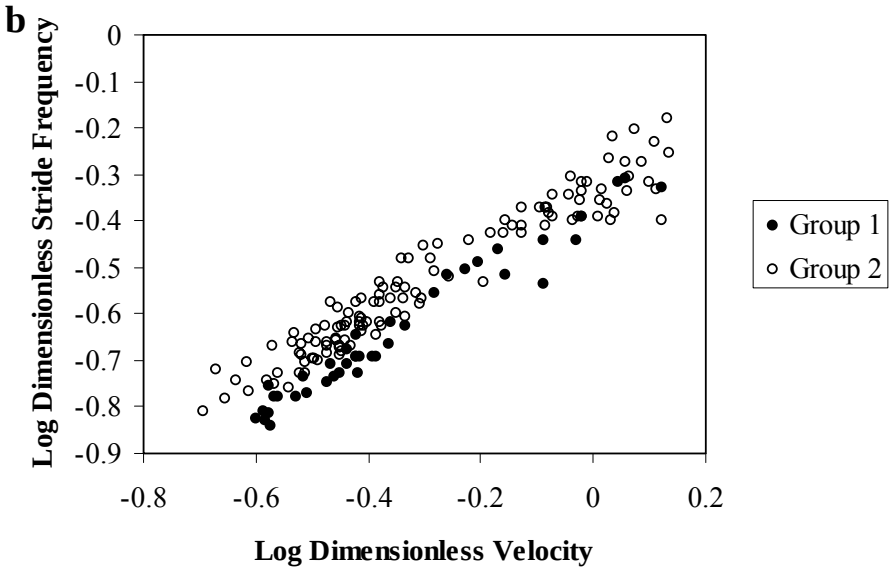


Figure 4.11b. Between group comparisons of dimensionless stride frequencies in Infant 2.

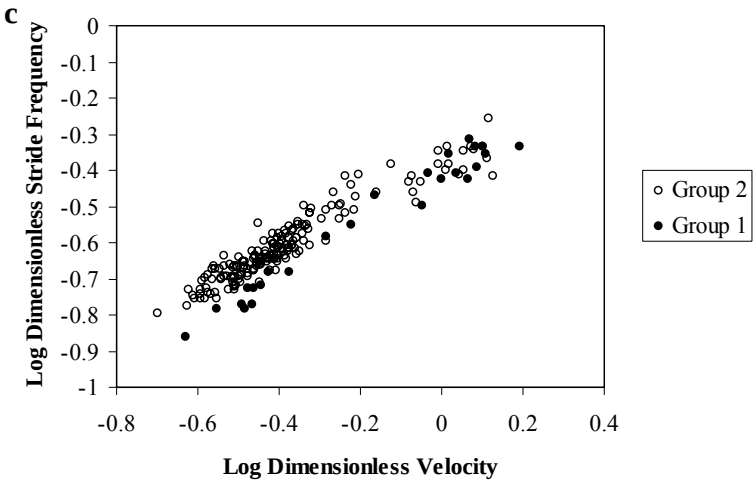
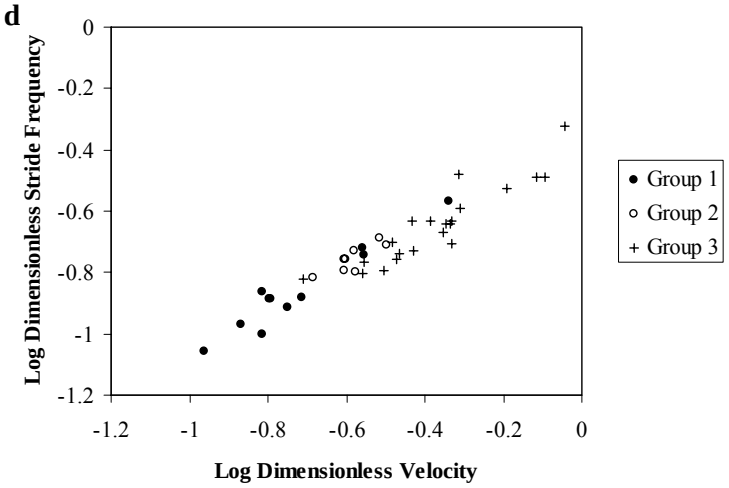


Figure 4.11c. Between group comparisons of dimensionless stride frequencies in Infant 3.



Figures 4.11d. Between group comparisons of dimensionless stride frequencies in Infant 3.

Group 1 for all individuals is represented by closed circles, Group 2 for all individuals is represented by open circles, Group 3 for Infant 4 is represented by open triangles. Dimensionless stride frequencies are significantly lower in Group 1 compared to Group 2 for Infant 1 (a) and Infant 2 (b) and at low dimensionless speeds in Infant 3 (c). Dimensionless stride frequencies do not significantly differ between groups in Infant 4 (d).

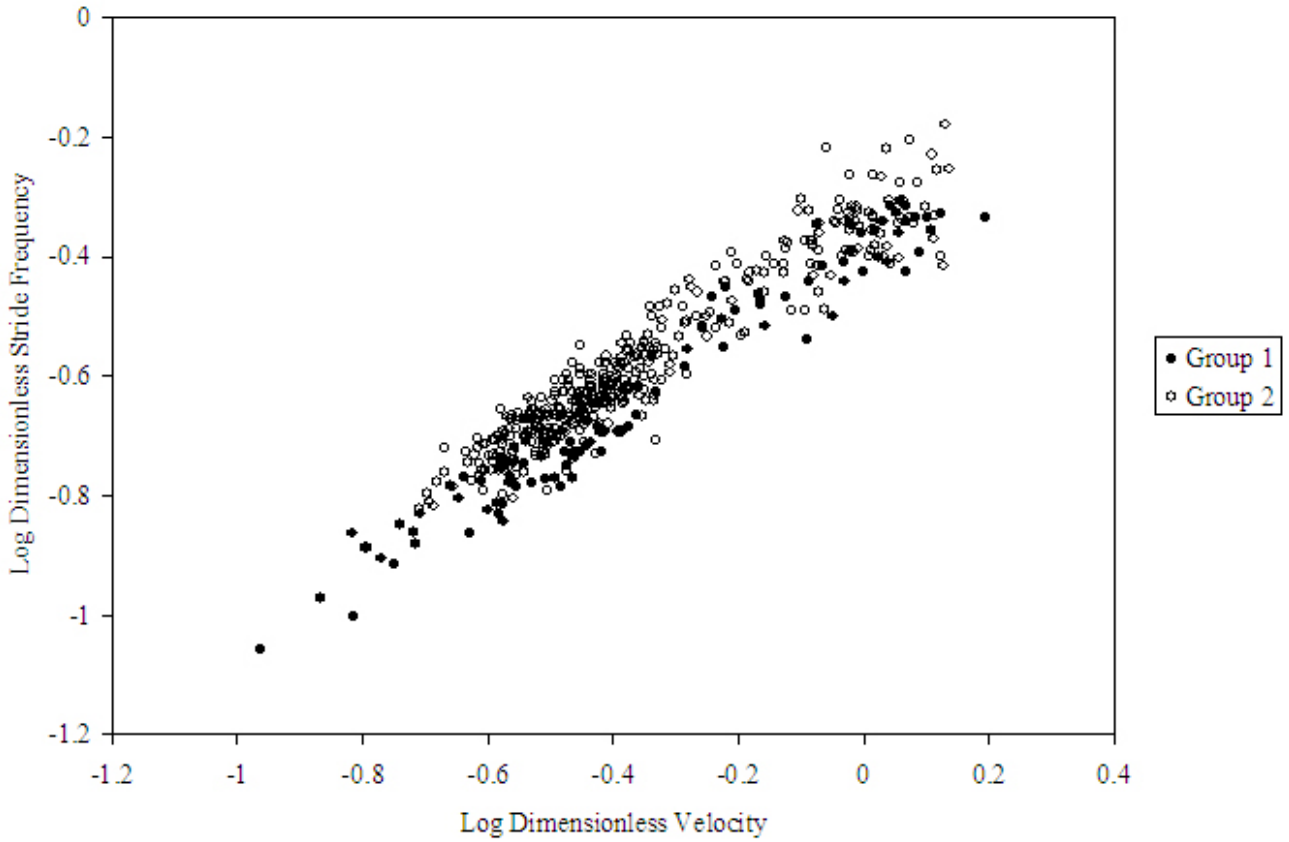
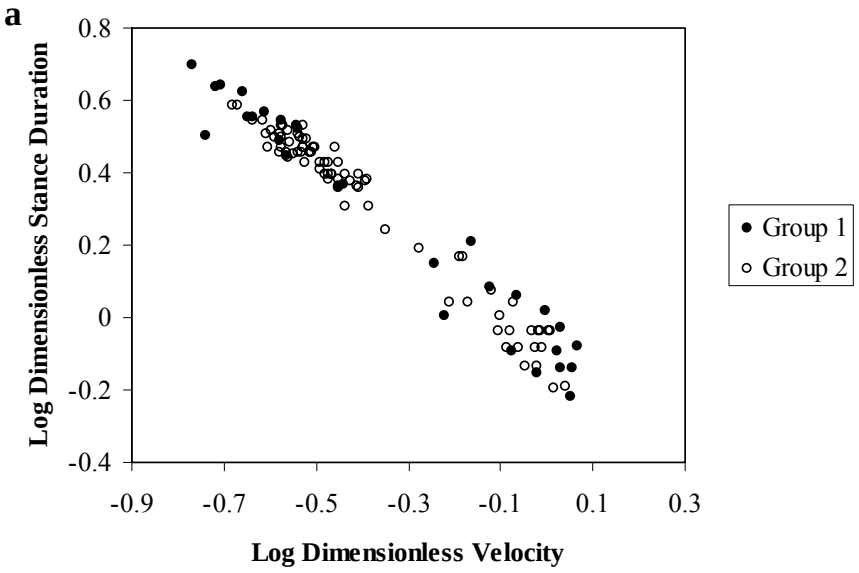
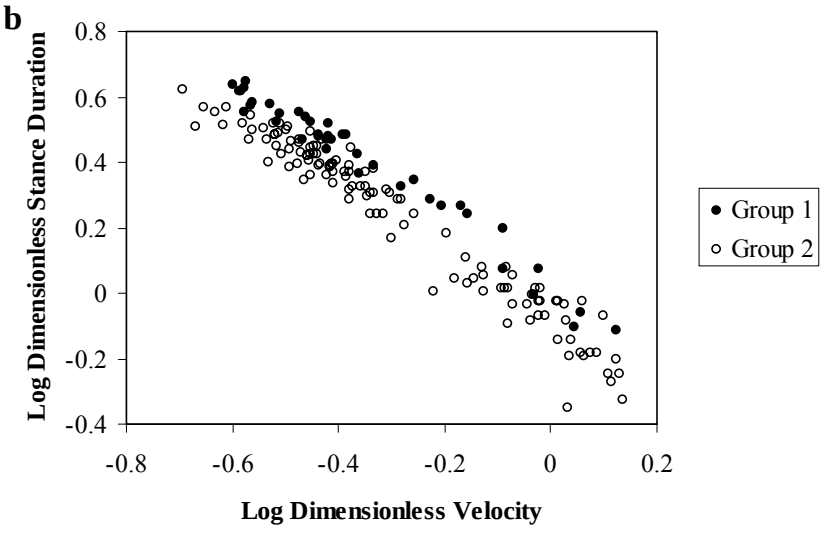


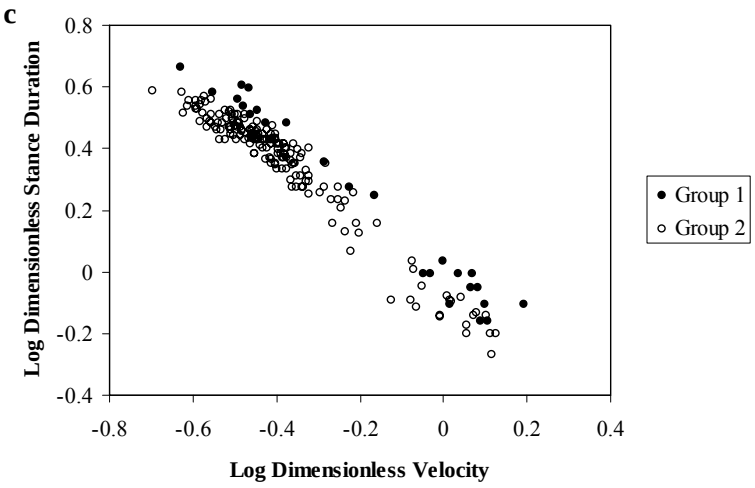
Figure 4.12. Between-group comparison of dimensionless stride frequencies over the entire dimensionless velocity range for the combined sample of infant baboons.



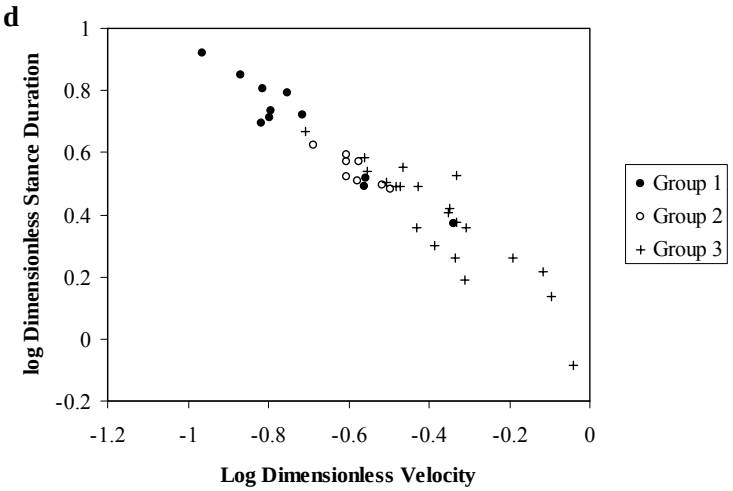
Figures 4.13a. Between group comparisons of dimensionless stance durations over the dimensionless velocity range in Infant 1.



Figures 4.13b. Between group comparisons of dimensionless stance durations over the dimensionless velocity range in Infant 2.

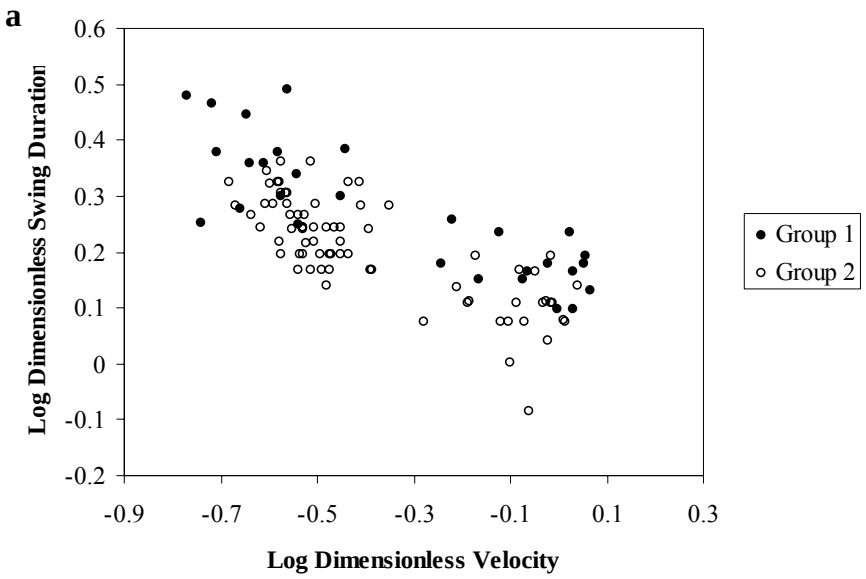


Figures 4.13c. Between group comparisons of dimensionless stance durations over the dimensionless velocity range in Infant 3.

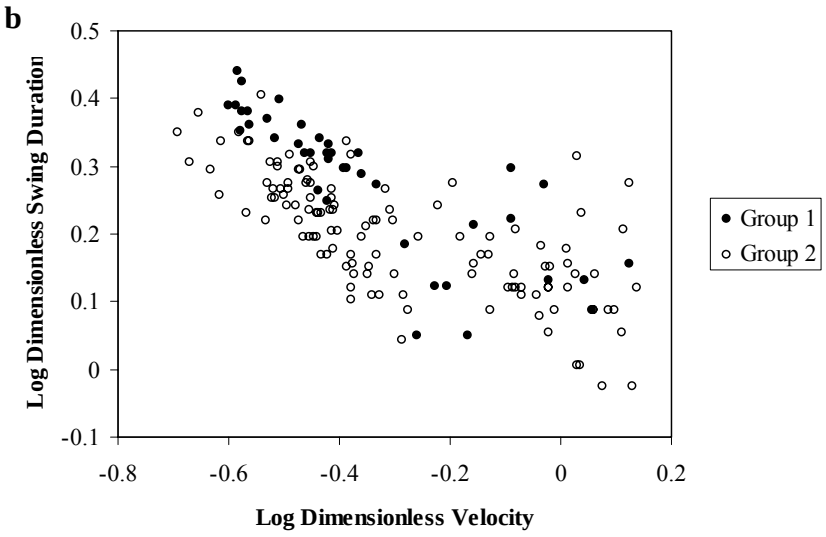


Figures 4.13d. Between group comparisons of dimensionless stance durations over the dimensionless velocity range in Infant 4.

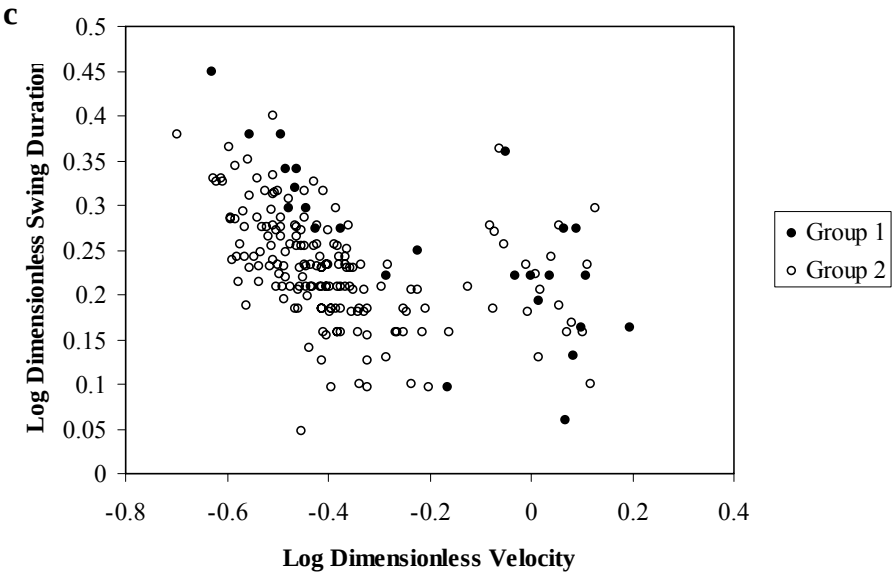
Group 1 for all figures is represented by closed circles, Group 2 for all individuals is represented by open circles, Group 3 of Infant 4 is represented by plus signs. Dimensionless stance durations do not significantly differ between groups for Infant 1 (a), are significantly longer in Group 1 compared to Group 2 for Infant 2 (b) and Infant 3 (c). Dimensionless stance durations do not differ between groups in Infant 4 (d).



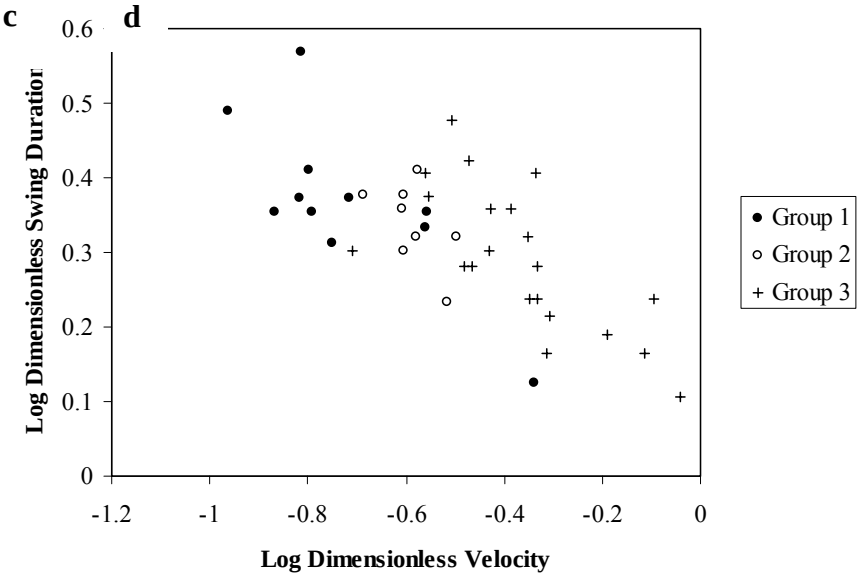
Figures 4.14a. Between group comparisons of dimensionless swing durations over the range of dimensionless velocities in Infant 1.



Figures 4.14b. Between group comparisons of dimensionless swing durations over the range of dimensionless velocities in Infant 2.



Figures 4.14c. Between group comparisons of dimensionless swing durations over the range of dimensionless velocities in Infant 3.



Figures 4.14d. Between group comparisons of dimensionless swing durations over the range of dimensionless velocities in Infant 4. Group 1 for all individuals is represented by closed circles, Group 2 for all individuals is represented by open circles, Group 3 for Infant 4 is represented by plus signs. Dimensionless swing durations are significantly longer in Group 1 compared to Group 2 for Infants 1 (a), 2 (b), and 3 (c). Dimensionless swing durations do not significantly differ between groups in Infant 4 (d).

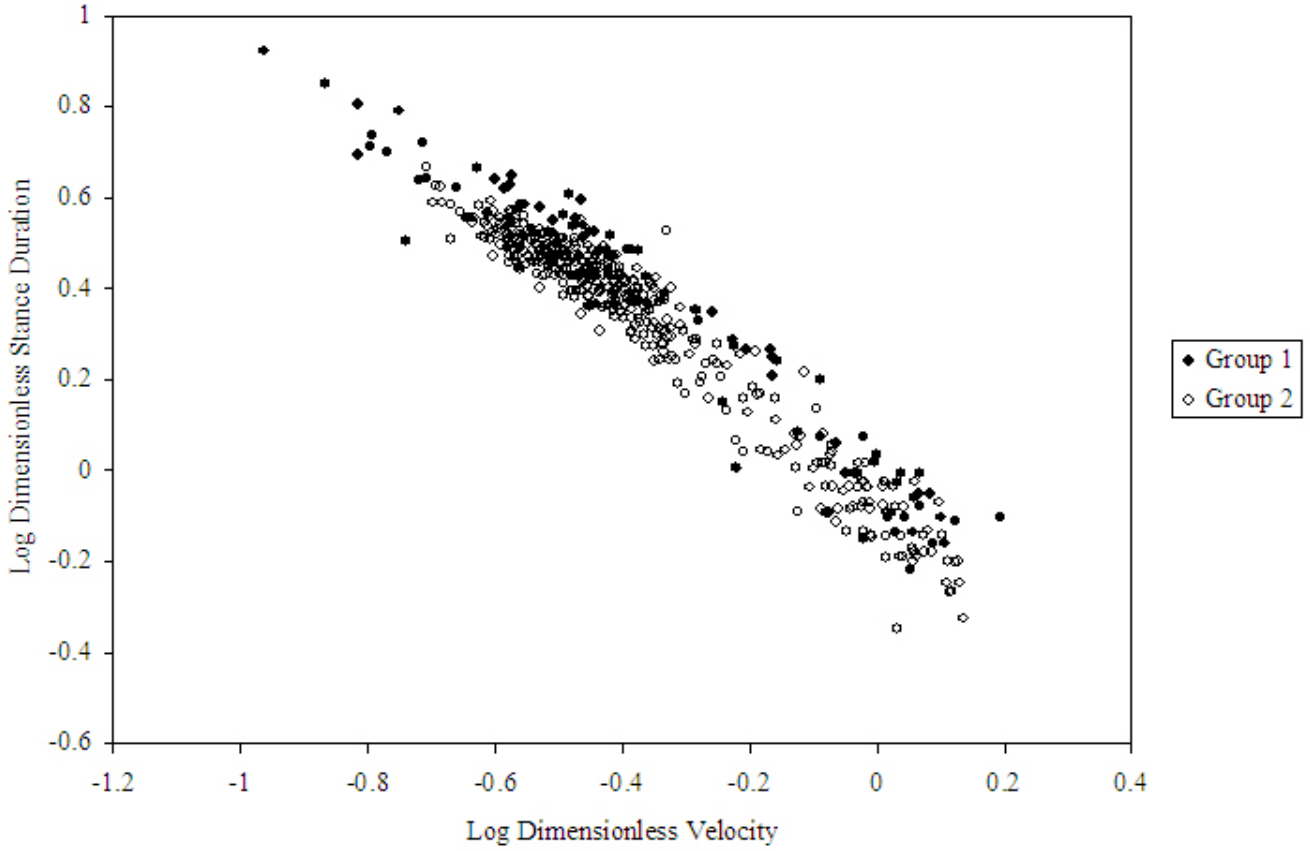


Figure 4.15. Dimensionless stance duration over the range of dimensionless velocities in the combined infant baboon sample.

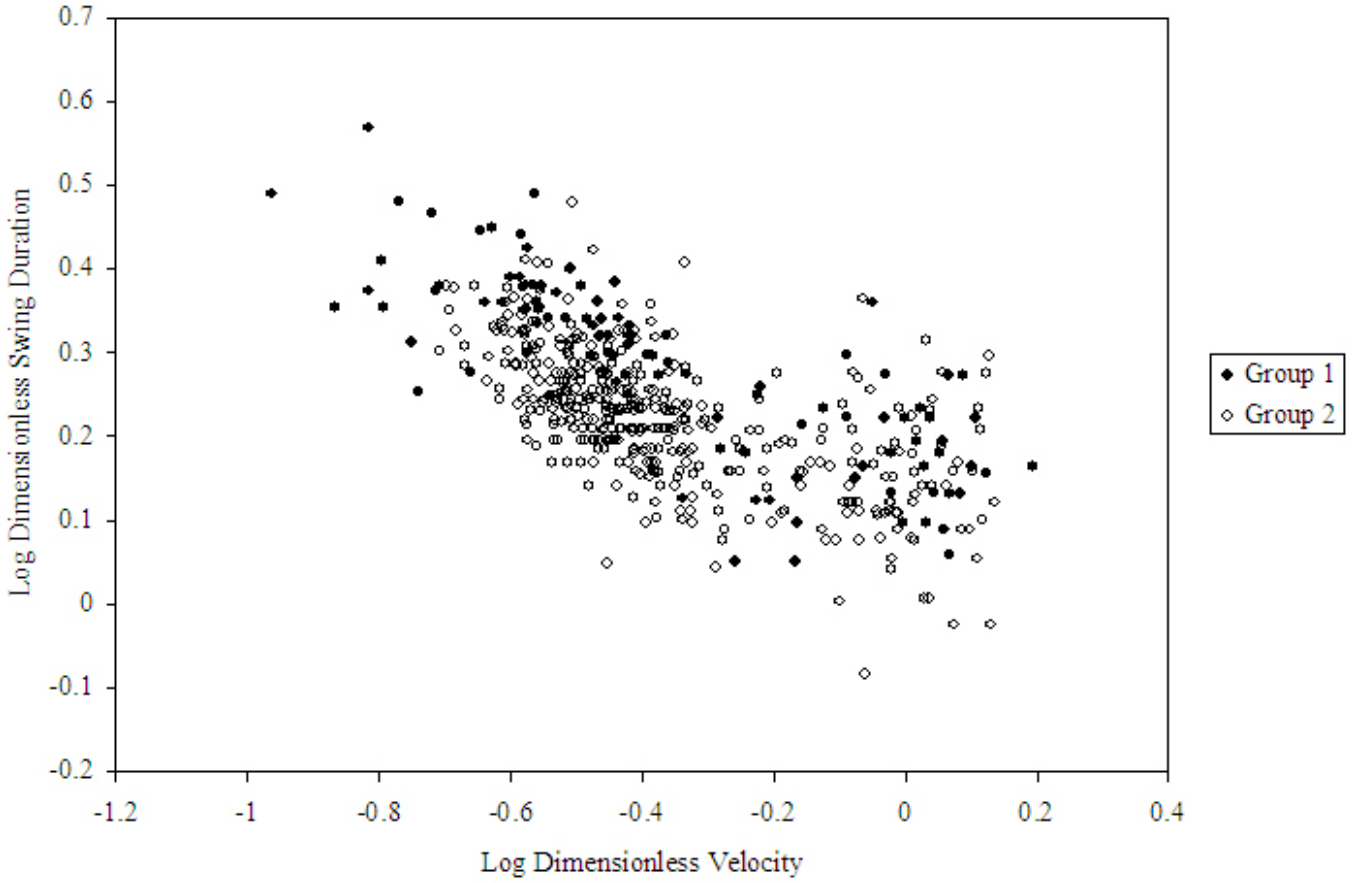
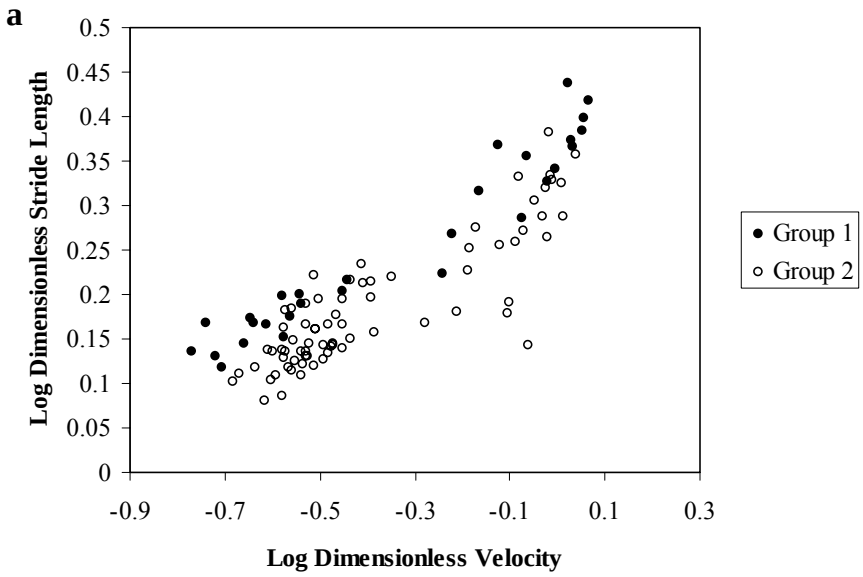
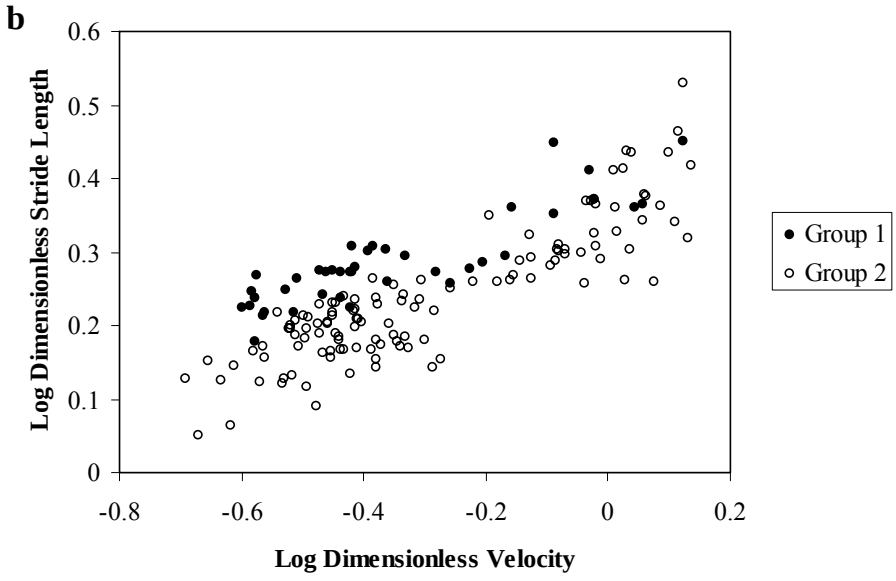


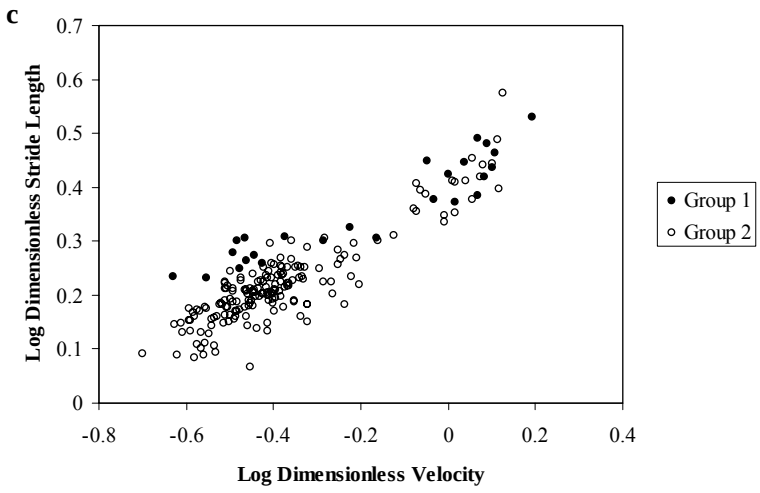
Figure 4.16. Dimensionless swing durations over the entire dimensionless speed range for the combined infant baboon sample.



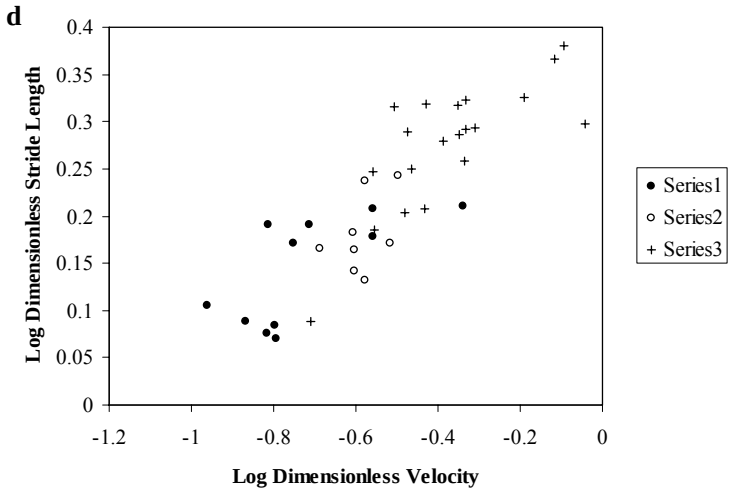
Figures 4.17a. Between group comparisons of dimensionless stride lengths over the entire dimensionless velocity range in Infant 1.



Figures 4.17b. Between group comparisons of dimensionless stride lengths over the entire dimensionless velocity range in Infant 2.



Figures 4.17c. Between group comparisons of dimensionless stride lengths over the entire dimensionless velocity range in Infant 3.



Figures 4.17d. Between group comparisons of dimensionless stride lengths over the entire dimensionless velocity range in Infant 4.

Group 1 for all individuals is represented by closed circles, Group 2 for all individuals is represented by open circles, Group 3 for Infant 4 is represented by plus signs. Dimensionless stride lengths are significantly longer in Group 1 compared to Group 2 for Infants 1 (a), 2 (b), and 3 (c). Dimensionless stride lengths do not significantly differ among the three groups for Infant 4 (d).

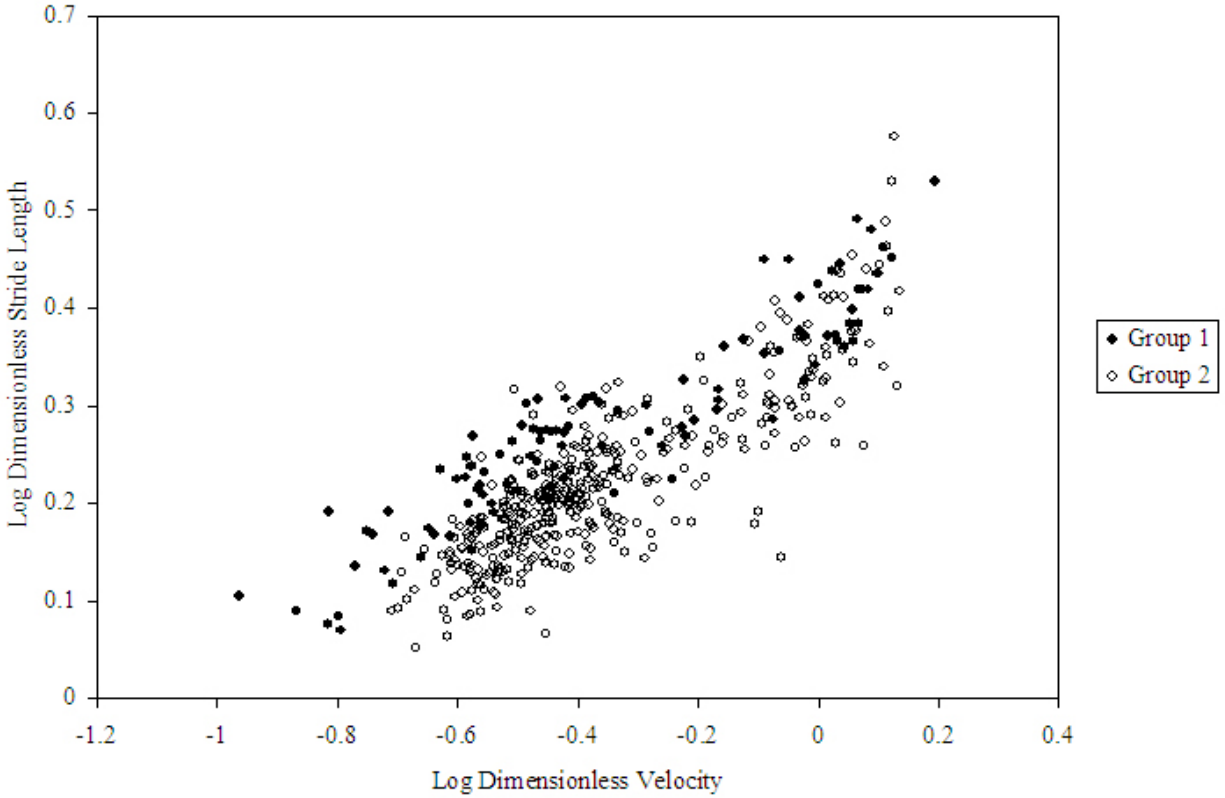


Figure 4.18. Between group comparison of dimensionless stride lengths over the dimensionless velocity range in the combined sample of infant baboons

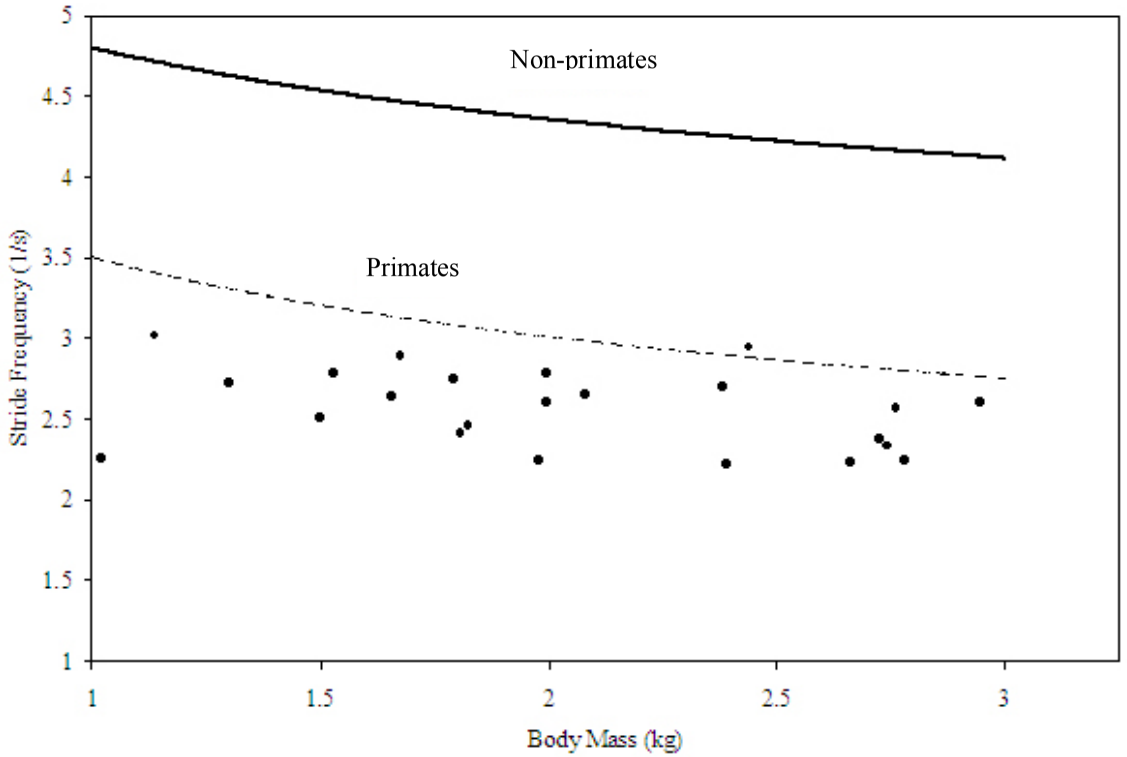


Figure 4.19. Stride frequencies at the trot-gallop transition for the infant baboons, adult primates, and non-primate quadrupeds. Adult primate (dashed line) and non-primate (solid line) data from Alexander and Maloiy (1984). Infant baboon data (closed circles) are predicted stride frequencies at their predicted trot-gallop transition velocities. See text for further details.

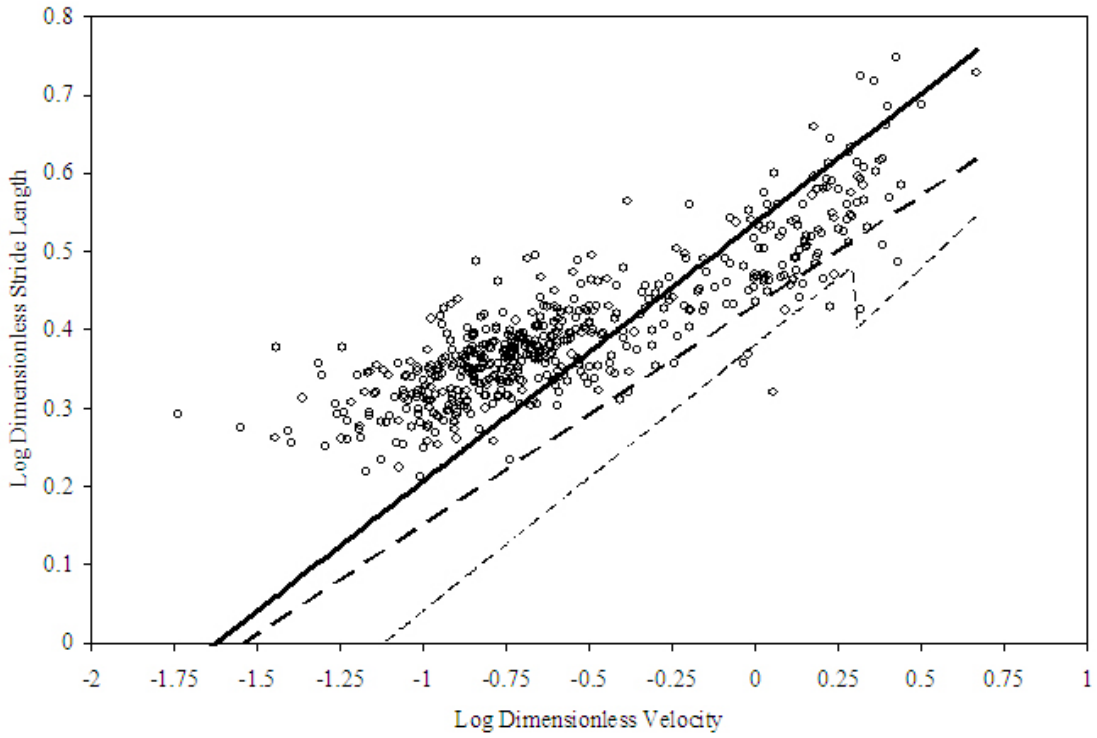


Figure 4.20. Dimensionless stride lengths in the infant baboons, adult primates, and non-primate quadrupeds. Infant baboons (open circles); Adult primates (solid black line), non-primate non-cursorial quadrupeds (dashed thick black line), and non-primate cursorial quadrupeds (dashed thin black line) data from Alexander and Maloiy (1984).

CHAPTER 5

Effects of limb mass distribution on mechanical work and power during quadrupedalism

INTRODUCTION

The effect of limb mass distribution on the energetics of quadrupedalism is a highly debated topic (see Taylor et al., 1974; Hildebrand, 1985; Hildebrand and Hurley, 1985; Myers and Steudel, 1985; Steudel, 1990). Theoretically, relatively distal limb mass concentrations should increase energetic costs due to increases in the amount of work that must be done to move limb segments relative to the body (internal work; see Hildebrand and Hurley, 1985; Dellanini et al., 2003). Large distal muscles should also reduce the length of distal tendons necessary for storage and release of elastic strain energy, which should increase energetic costs during running (Alexander et al., 1981; Preuschoft and Gunther, 1994). However, Taylor et al. (1974) showed that three mammals that differed greatly in their limb mass distributions (the cheetah, the gazelle, and the goat) did not differ significantly in their energetic costs of locomotion at a given velocity. Additionally, primate quadrupeds do not differ from other mammalian quadrupeds in their energetic costs of locomotion at a given velocity despite their relatively distal limb mass concentrations (Taylor et al., 1982; Heglund, 1985; Steudel-Numbers, 2003).

The conflicts between theory and empirical results would be difficult to reconcile if all mammalian quadrupeds walk with dynamically similar kinematics. Mammalian quadrupeds, however, do not all walk with dynamic similarity (see Alexander and Jayes,

1983; Alexander and Maloiy, 1984; Chapter 4). Limb mass distribution was shown to greatly impact locomotor kinematics in Chapters 3 & 4. Individuals with relatively distal limb mass concentrations walk with relatively long strides and relatively low stride frequencies at a given dimensionless velocity.

Stride frequency may have a large impact on mechanical internal work (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995; Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004). Low stride frequencies reduce the velocity at which muscles and tendons must move a limb, thereby reducing internal work (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995; Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004). It is possible that the use of relatively low stride frequencies may in fact mitigate the negative impact of distal muscle mass distributions on internal work.

Low stride frequencies can also have important effects on the work done to raise and accelerate the body center of mass relative to its surroundings (external work; see Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995; Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004). For example, Cavagna and Franzetti (1986) showed that when humans lowered their stride frequencies at a given velocity, they used longer strides and external work increased (see also Cavagna et al., 1991). Long strides increase the vertical displacement of the center of mass, causing the muscles and tendons to do a larger amount of external work (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995; Schepens et al., 2001; Heglund and Schepens, 2003; Schepens et al., 2004).

Humans tend to choose a stride frequency that minimizes total work through a tradeoff between the effects of stride frequency on internal work and the effects of stride length on external work (Cavagna and Franzetti, 1986; Cavagna et al., 1991; Minetti et al., 1995). It is possible that a tradeoff between internal and external work occurs for a quadruped based on its limb mass distribution patterns. Relatively low stride frequencies reduce internal work, while the relatively long strides increase external work, so that the amount of total work done by muscles and tendons to move the body (the sum of internal and external work) is not relatively large in quadrupeds with relatively distally distributed limb mass. The use of such a tradeoff mechanism to minimize total work was tested in this study using the ontogenetic sample of infant baboons.

Additionally, it has been suggested that the limb mass distribution patterns of primates reduce their abilities to store and recover elastic energy during running trots (Alexander et al., 1981; Preuschoft and Gunther, 1994). If true, then either primates would avoid trotting, or they would have increased energy expenditures during these gaits compared to other mammals. As discussed earlier, primates do not appear to differ from other mammals in their energetic costs (Taylor et al., 1982; Heglund, 1985; Steudel-Numbers, 2003), so avoidance of running trots is a reasonable alternative (Preuschoft and Gunther, 1994). Schmitt et al. (2003) suggested that primates use an amble at running velocities, which differs in footfall sequence compared to the trot. Reilly and Biknevicius (2003) have discussed the importance of footfall sequence in center of mass energy changes. It is possible that the amble represents a compromise footfall pattern that allows primates to save energy by pendular means, rather than elastic energy storage

and recovery. The use of the amble will be explored in this sample of infant baboons and possible energy savings provided by the amble are discussed.

Hypotheses

It was predicted that as the infant baboons age, and their limb mass distributions migrate proximally, mechanical work and power will follow the tradeoff mechanism described above. At young ages, when mass is most distal and individuals use relatively low stride frequencies at a given velocity, the infant baboons should do lower amounts of internal work and power, higher amounts of external work and power, and similar amounts of total work and power compared to older age groups. The results from this study were also compared to data for non-primate quadrupeds from Fedak et al. (1982) and Heglund et al. (1982). It was predicted that, compared to non-primate cursorial quadrupeds, the infant baboons will have lower values of internal work and power, higher values of external work and power, and similar values of total work and power.

METHODS

Sample

Four infant baboons (*Papio cynocephalus*) were obtained from the Southwest Foundation for Biomedical Research (SFBR) from a population rejected by their mothers and placed in the SFBR nursery. Infant baboons were housed at the University of Texas Animal Resource Center using methods approved by both the University of Texas institutional animal care and use committee (IACUC) and the SFBR IACUC.

Kinematics

The collection of three-dimensional segmental kinematics was described in Chapter 4. Three dimensional marker positions were filtered using the Vicon moving average filter. The same kinematics data were used to calculate mechanical work and power values in the infant baboon sample.

Inertial properties

Limb inertial properties were calculated for each infant prior to kinematics data collection. All segment inertial properties were calculated for infant baboons using methods described in Chapter 2 and in the appendix.

Internal mechanical work and power

As described earlier, the total positive work that must be supplied by muscles and tendons during locomotion (W_{tot}) can be divided into two parts (Fenn, 1930). The first part is the mechanical work required to move body segments relative to the whole body center of mass (internal work; W_{int}) first described by Fenn (1930). W_{int} is calculated from changes in each segment's energy over an entire stride (after Fedak et al., 1982; Willems et al., 1995). The second part of W_{tot} is the work that must be supplied to lift and accelerate the whole body center of mass (external work; Cavagna et al., 1977) and its calculation is described in a later section.

The kinetic and potential energy of each body segment relative to the body center of mass was calculated from the 3-D marker positions captured by the Vicon motion analysis system. For each stride, one side of the body (side facing cameras or ipsilateral

side) was divided into 5 segments that were defined by passive reflective markers at each of the major joints (trunk, arm, forearm, thigh, leg). These segment definitions were consistent with those used for the calculation of segment inertial properties in Chapter 2. Affixing markers to define the hand and foot segments was problematic both because of the small size of the individuals' hands and feet, and because the infant baboons were more likely to remove those markers. For this analysis, the hands and feet were considered point masses at the ends of the forearms and lower legs respectively and the head was considered a point mass at the cranial end of the trunk.

The positions and velocities for segments on the contralateral side of the body were estimated assuming the movements of the contralateral side segments during half a stride were the same as the movements of the ipsilateral segments during the other half of the stride (see also Fedak et al., 1982; Willems et al., 1995). The touchdowns for the contralateral forelimb and hindlimb were taken from the video data. Contralateral side segment movements were then estimated by first, calculating for each instant in time, the percentage of time that had elapsed from limb touchdown. Next, the position of the comparable ipsilateral segment at this percentage of stride duration from its limb touchdown was assigned to the contralateral segment. This procedure was repeated for every instant of time for each stride.

The whole body center of mass (CM) position was calculated from segment positions and their masses and centers of mass as follows:

$$CM_x = \frac{\sum m_i d_{ix}}{\sum m_i} \qquad (5.1)$$

where m_i is the mass of the ith segment and d_{ix} is the position of the center of mass of the ith segment from the calibrated origin of the viewing volume in the x direction. This procedure was replicated for the y and z directions to obtain a 3-dimensional CM position.

The translational and rotational velocity of each segment's center of mass relative to the whole body center of mass was calculated using the finite difference method (see Winter, 1979):

$$v_{x,i} = \frac{x_{i+1} - x_{i-1}}{2\Delta t} \tag{5.2}$$

where $v_{x,i}$ is the velocity of the ith segment in the x direction, and Δt is the time between two adjacent samples (x_i and x_{i+1}). This process was then repeated to calculate translational and rotational (substitute segment angle for x in equation 5.2) segment velocities in all directions.

The translational ($E_{k,trans}$; Joules) and rotational ($E_{k,rot}$; Joules) kinetic energy of each segment relative to the whole body center of mass was then calculated for each frame of each stride using the following equations (after Fedak et al., 1982; Willems et al., 1995):

$$E_{k,trans,i} = \frac{1}{2} m_i v_i^2 \tag{5.3}$$

$$E_{k,rot,i} = \frac{1}{2} I_i \omega_i^2 \tag{5.4}$$

where m_i is the ith segment's mass (kg), v_i is the ith segment's velocity relative to the whole body center of mass (m/s), I_i is the ith segment's mass moment of inertia about its

center of mass (kg m^2), ω_i is the ith segment's angular velocity (radians/s). $E_{k,trans,i}$ and $E_{k,rot,i}$ were summed at each instant in time to obtain the segment energy ($E_{k,i}$). $E_{k,i}$'s for both segments of a limb were summed at each instant in time to calculate the total energy of each limb ($E_{k,limb}$). The sum of the positive changes in each limb's kinetic energy curve was calculated over an entire stride (see Fig. 5.1 for example of this procedure). $E_{k,limb}$ for all limbs were then summed to calculate the mechanical internal work needed to move the limbs relative to the body.

This method of calculating internal work allows for transfers of energy between segments of a single limb, but not between limbs. There is no known mechanism to allow for transfers of energy between limbs (see Fedak et al., 1982), so this value represents the best estimate of the positive work needed to move the limbs relative to the body. This value was divided by body mass to obtain the mass specific internal work (W_{int}). Mass specific internal work was divided by stride duration to obtain the mass specific internal power ($\dot{W}_{int}$) that must be supplied by the muscles and tendons to move the limbs relative to the body.

The internal work due to changes in limb potential energy is usually a very small component of a segment's energy (Willems et al., 1995) and is often ignored all together (Fedak et al., 1982). Cavagna and Kaneko (1977) and Willems et al. (1995) suggest that this term may be neglected because the kinetic energy of a segment is sufficient to sustain its vertical movements.

External mechanical work and power

The positive work done to raise and accelerate the whole body center of mass was calculated using segmental kinematics to reconstruct center of mass movements after Minetti et al. (1999). The position of the center of mass was calculated according to equation 5.1. The velocity of the center of mass (V_{cm}) was calculated using the finite differences method (eq. 5.2; see also Winter, 1979). The instantaneous kinetic energy of the center of mass ($E_{k,cm}$) in both forward (f) and vertical (v) directions was calculated as:

$$E_{f,k,cm} = \frac{1}{2} M_{cm} V_{f,cm}^{2} \quad (5.5)$$

$$E_{v,k,cm} = \frac{1}{2} M_{cm} V_{v,cm}^{2} \quad (5.6)$$

The instantaneous potential energy of the center of mass was calculated as:

$$E_{p,cm} = M_{cm} g H_{cm} \quad (5.7)$$

where M_{cm} is body mass and H_{cm} is the height of the center of mass. Potential and kinetic energies were summed at each instant in time to obtain the total energy of the center of mass (E_{cm}). Mass-specific external mechanical work (W_{ext}) was calculated as the sum of the positive increments in the E_{cm} curve over an entire stride divided by body mass. Mass specific external power ($\dot{W}_{ext}$) was calculated as $\frac{W_{ext}}{StrideDuration}$.

Potential and kinetic energy can be exchanged if they are out of phase with each other (see Chapter 1, Fig. 1.2a; see also Cavagna et al., 1977). This energy exchange reduces W_{ext} and its amount is calculated as the percent of energy recovered (after Cavagna et al., 1977):

$$\%\,\mathrm{Recovery} = \left(\frac{\Delta E_{k,cm} + \Delta E_{p,cm} - \Delta E_{cm}}{\Delta E_{k,cm} + \Delta E_{p,cm}} \right) \times 100 \qquad (5.8)$$

where $\Delta E_{k,cm}$, $\Delta E_{p,cm}$, ΔE_{cm} are the sums of the positive changes in the kinetic, potential, and total energy curves over each stride respectively. Percent recovery is then the difference between the amount of work that would have been done with no energy exchange ($\Delta E_{k,cm} + \Delta E_{p,cm}$) and the amount of work actually done (ΔE_{cm}) as a percentage of the work that would have been done with no exchange.

Total mechanical work and power

Total mechanical work was calculated as the sum of W_{int} and W_{ext} (Heglund et al., 1982; Willems et al., 1995). Total mechanical power was calculated as the sum of $\dot{W}_{int}$ and $\dot{W}_{ext}$. This method of calculating total work and power assumes no transfer of energy between internal and external energies and is accepted as a reasonable estimate of the total work and power that must be supplied by the muscles and tendons to move the body and body segments during locomotion (see Heglund et al., 1982; Willems et al., 1995).

Footfall sequence

To address the possibility that footfall sequence and timing may impact the amount of energy recovered by pendular mechanisms (see Reilly and Biknevicius, 2003), gait numbers were calculated for each stride after Hildebrand (1966; see also Shapiro and Raichlen, in press). The gait number is the amount of time between a hindlimb touchdown and the next ipsilateral forelimb touchdown as a percentage of stride duration.

Gait numbers of exactly 0 or 100 indicate the *ipsilateral* forelimb and hindlimb touchdowns occur at the same time, and represent a pace. Gait numbers of exactly 50 indicate that the hindlimb and the *contralateral* forelimb touchdowns occur at the same time, and represent a trot. All other gait numbers indicate some degree of forelimb and hindlimb decoupling, with gait numbers greater than 50 indicating a hindlimb touchdown followed by a contralateral forelimb touchdown (diagonal sequence gait) and gait numbers less than 50 indicating a hindlimb touchdown followed by an ipsilateral forelimb touchdown (lateral sequence gait). A complete decoupling of forelimbs and hindlimbs occurs at gait numbers of 25 and 75, termed single-foot gaits. In these gaits, forelimb and hindlimb touchdowns are evenly spaced in time.

Statistical analyses

Age groupings used to compare changes in mechanical work and power during ontogeny were the same as those used for kinematic analyses. For all analyses, Group 1 represents ages where limb mass is relatively distally distributed and Group 2 represents ages with a more proximal concentration of limb mass. For each variable, ANCOVA was used to compare variables between groups with velocity or dimensionless velocity as the covariates. Significant differences were determined using Tukey-Kramer post-hoc tests to account for multiple comparisons.

RESULTS

Internal energy changes

Before describing how W_{int} and $\dot{W}_{int}$ change with limb mass distribution, the changes in the mechanical energy of each limb segment during a stride will be described. Figures 5.2-5.4 show examples of changes in each segment's kinetic energy over a single stride at three different velocities representing the variation in energy changes over the three major quadrupedal gaits: walks, runs, and gallops.

At all velocities, the kinetic energy changes are much more drastic in the distal segments compared to the proximal segments. Although distal segments are generally lighter than the proximal segments (see Chapter 2), they must travel through a greater distance, and therefore move at a higher velocity compared to the proximal segments (Fedak et al., 1982). Any increase in the mass of these distal elements will therefore increase the total kinetic energy of the limb to a greater degree than increases in proximal segment mass, because its velocity is higher than the proximal segment. As velocity increases, peak kinetic energy values also increase, due to increases in limb velocity (note the scale of kinetic energy changes in the three figures).

During walking, comparable segments in the forelimb and hindlimb reach similar peak kinetic energy values (Fig. 5.2). This similarity in peak kinetic energy is also found between the forelimb and hindlimb. These results are similar to those reported for other quadrupedal mammals (see Fedak et al., 1982). At running velocities, peak limb kinetic energies are higher than those at walking velocities (Fig. 5.3). Finally, at galloping

velocities, peak segment and whole limb kinetic energy is higher than at slower velocities (Fig. 5.4). Hindlimb peak kinetic energy is higher than the forelimb.

The results for running and galloping velocities are also similar to those obtained for other mammalian quadrupeds (see Fedak et al., 1982). As in other quadrupeds, the increase in peak energy magnitudes for all limb segments with increasing velocity indicates that the internal work and power should also increase with increasing velocity in the infant baboon sample.

Internal work and power

Internal work and power in the sample of infant baboons is first examined as a function of raw velocity. Internal work is significantly lower at younger ages (Group 1) in Infant 1 when velocity is taken into account (Figs. 5.5a; Table 5.1). This between group difference is mainly driven by the lower internal work values for Group 1 at high velocities.

Internal work does not differ significantly between groups in Infant 2 (Fig. 5.5b; Table 5.1). Stride frequencies are slightly lower at low velocities for this infant baboon at young ages (Group 1; see Chapter 4, Fig. 4.9b), and may therefore mitigate the effects of her distal limb mass on W_{int}.

Internal work is significantly higher in Group 1 compared to Group 2 for Infant 3 (Fig.5.5c; Table 5.1). Again, these results are consistent with the comparison of raw stride frequencies between groups for Infant 3 in Chapter 4 (see Chapter 4, Fig. 4.9c). Infant 3 used slightly higher stride frequencies at higher velocities in Group 1, driving its internal work values higher at younger ages.

Internal work is significantly lower in Group 1 of Infant 4 compared to Group 3 (Fig. 5.5d; Table 5.2). Internal work for Group 2 does not differ significantly from Groups 1 and 3 (Fig. 5.5d; Table 5.2). These results should be taken with caution as velocities overlap only slightly between groups for Infant 4. Finally, when all individuals are combined, internal work shows no significant between group differences over the raw velocity range (Fig. 5.6; Table 5.3).

Internal power is significantly lower in Group 1 for Infant 1 (Fig. 5.7a; Table 5.1). Internal power requirements do not significantly differ between groups for Infant 2 (Fig. 5.7b; Table 5.1). Internal power requirements are significantly higher in Group 1 for Infant 3 compared to Group 2 (Fig. 5.7c; Table 5.1). Internal power requirements do not differ significantly between any of the sampled age ranges for Infant 4 (Fig. 5.7d; Table 5.4).

Finally, when all individuals are combined, internal power shows no significant between group differences over the raw velocity range (Fig. 5.8; Table 5.3).

Internal work and power requirements were also compared between groups over similar dimensionless velocities. Internal work is significantly lower in Group 1 compared to Group 2 for Infant 1 (Fig. 5.9a; Table 5.1). Internal work does not differ significantly between groups for Infants 2 and 3 (Figs. 5.9b & 5.9c; Table 5.1). For Infant 4, internal work is significantly lower in Groups 1 and 2 compared to Group 3 (Fig. 5.9d; Table 5.5). Infant 4's internal work does not differ significantly between Groups 1 and 2 (Fig. 5.9d; Table 5.5).

Finally, when all individuals are combined, internal work is significantly lower in Group 1 individuals compared to Group 2 over the dimensionless velocity range (Fig.

5.10; Table 5.3). The significantly lower values of internal work are driven mainly by Infant 1's lower Group 1 internal work values (see Fig. 5.9a).

Mechanical internal power is significantly lower at younger ages in Infant 1 after dimensionless velocity is taken into account (Fig. 5.11a; Table 5.1). Mechanical internal power requirements do not significantly differ between groups in Infants 2-4 (Figs. 5.11b -5.11d; Table 5.1 & Table 5.6).

Finally, when all individuals are combined, internal power is significantly lower in Group 1 individuals compared to Group 2 over the dimensionless velocity range (Fig. 5.12; Table 5.3). As is the case for internal work, the significantly lower values of internal power when dimensionless velocity is the covariate are driven mainly by Infant 1's lower Group 1 internal power values (see Fig. 5.11a).

Manipulation of limb inertial properties in internal energy calculations

A manipulation of inertial properties was performed to examine how sensitive W_{int} is to an individual's segment inertial properties. This manipulation consisted of scaling the segment inertial properties of all Group 2 individuals to those of Infant 2 at 1.97 months (a Group 1 age that is the most distal limb mass distribution pattern recorded for the infant sample). The following equations were used to scale segment inertial properties of older individuals (2) to those of Infant 2 at 1.97 months (1):

$$m_{scaled} = M_2 \times \frac{m_1}{M_1} \tag{5.9}$$

$$cm_{scaled} = l_2 \times \frac{cm_1}{l_1} \tag{5.10}$$

$$I_{scaled} = m_2 l_2 \times \frac{I_1}{m_1 l_1^2} \quad (5.11)$$

where M_2 is the Group 2 individual's body mass, m_1 is Infant 2's segment mass at 1.97 months, M_1 is Infant 2's body mass at 1.97 months, l_2 is the Group 2 individual's segment length, cm_1 is Infant 2's segment center of mass position from the proximal end of the segment, l_1 is Infant 2's segment length at 1.97 months, and I_1 is Infant 2's segment mass moment of inertia about its center of mass at 1.97 months.

W_{int} was recalculated for each stride of all Group 2 individuals using scaled segment inertial properties. If older individuals have the limb mass distributions of younger individuals, but do not reduce their stride frequencies, they would have higher W_{int} values at a given velocity (Fig. 5.13). W_{int} values are, on average, 20% larger in the manipulated sample (calculated as the absolute value of the difference between actual and manipulated values as a percentage of actual values). So, by using low stride frequencies when their mass is most distal, the infant baboons save approximately 20% of the mechanical energy they would otherwise have had to output to move their limbs relative to their body.

Energy changes of the whole body center of mass

Prior to examining external work and power in the infant baboon sample, kinetic and potential energy changes of the whole body CM are presented. It is important to note how the shapes of the curves change with speed in order to understand how individuals may substitute exchange between potential and kinetic energy, or elastic energy storage and recovery, for muscular work.

Energy changes of the whole body CM are highly dependent on velocity. As described earlier, walking is characterized by an out of phase relationship between the CM's potential and kinetic energy (Cavagna et al., 1977). Figure 5.14 shows the gravitational potential and kinetic energy changes during a single representative walking stride (v = .50 m/s) of an infant baboon. Gravitational potential and kinetic energy are almost completely 180 degrees out of phase.

It is clear from this phase difference that potential energy may easily be converted into forward kinetic energy, and vice versa by means of a pendular exchange between the two. At hindlimb touchdown, forward kinetic energy is highest and potential energy is lowest. As the individual enters stance phase, its body vaults over the forelimb and hindlimb in ground contact, and potential energy increases as kinetic energy decreases. Kinetic energy may therefore be converted into potential energy during this early part of stance phase. As the individual enters the second half of stance phase and falls over the stance limbs, this potential energy is converted into forward kinetic energy. This exchange reduces the amount of muscular work that must be provided by muscles and tendons to propel the individual.

Running gaits have been characterized as a spring-mass system (Cavagna et al., 1977; Farley et al., 1993). Figure 5.15 shows the gravitational potential and kinetic energy changes of this same individual at a running velocity (v= 1.14 m/s). (The running gait used by this individual for this figure is a trot: G = 54.8. Generally, gait numbers between 45 and 55 are called trots because of the extremely close diagonal limb coupling even though there may not be perfect synchronization (see Hildebrand, 1966). The addition of gait numbers that are not exactly 50 into this gait classification occurs because

there is some error in determining touchdown events. Despite the fact that primates have not been reported to use this gait, the infant baboons used it three times. Ambles will be discussed in a later section.) The difference between the phase relationships of potential and kinetic energy is drastic compared to walking. Potential and kinetic energy are largely in phase during running gaits. As the individual touches down, its fore- and hindlimbs compress (like springs) and both kinetic and potential energy decrease at the same time. During the second half of stance phase, the limbs re-extend, and potential and kinetic energy increase, again at the same time. Therefore, there is little chance for an exchange between potential and kinetic energy during these running gaits.

A reduction in the amount of muscular work needed to propel the animal must come from other mechanisms. The mechanism that has been suggested for running gaits is the storage and release of elastic energy in muscles and tendons. These elements are stretched (and energy is stored) as the limb compresses during the first half of stance phase, and release their stored energy during the second half of stance phase.

Potential and kinetic energy changes during galloping may re-introduce some pendular exchange, but mostly resemble the spring-like mechanism seen during running (Cavagna et al., 1977; Minetti, 1998). Figure 5.16 shows changes in potential and kinetic energy of the CM of this same individual at a galloping velocity (v = 2.4 m/s). Just after hindlimb touchdown, potential energy decreases, while kinetic energy increases. At this point, some pendular exchange is possible. After lift off, there is a slight increase in kinetic energy, but as the forelimbs touchdown, the body is decelerated, and both kinetic and potential energy decrease. Once the forelimbs lift off, kinetic energy begins decreasing again. So there is the possibility that some exchange in potential and kinetic

energy is possible during parts of a galloping stride, and that elastic mechanisms are in use during other parts of the stride.

External work and power

The positive changes in the summed potential and kinetic energy curves described above determine an individual's external work. External work and power were first compared between groups across raw velocities. External work did not differ significantly between age groups for Infants 1, 2, and 4 (Figs. 5.17a,b,d; Tables 5.1 & 5.7). External work was significantly higher in Group 1 compared to Group 2 for Infant 3 (Fig. 5.17c; Table 5.1). External work is significantly higher in Group 1 for the combined infant sample compared to Group 2 over the raw velocity range (Fig. 5.18; Table 5.3).

External power requirements are significantly higher in Group 1 for Infants 1 and 3 (Figs. 5.19a,c; Table 5.1). External power requirements do not differ significantly between age groups in Infants 2 and 4 (Figs. 5.19b,d; Table 5.1 & 5.8). External power is significantly higher in Group 1 for the combined infant baboon sample compared to Group 2 (Fig. 5.20; Table 5.3).

External work and power requirements were also examined after velocity was made dimensionless. None of the infant baboons show significant between group differences in mechanical external work (Figs. 5.21a-d; Table 5.1 & 5.9). External work does not show significant between group differences in the combined infant baboon sample over the dimensionless velocity range (Fig. 5.22; Table 5.3).

External power requirements show a similar pattern as external work in this sample of infant baboons. None of the infant baboons show significant between group differences in their external power requirements at a given dimensionless velocity (Figs. 5.23a-d; Table 5.1 & 5.10). External power does not show significant between group differences in the combined infant baboon sample over the dimensionless velocity range (Fig. 5.24; Table 5.3).

Total work and power

Total work and power were first compared between age groups across the entire raw velocity range. Total work does not differ significantly between groups for Infants 1,2 and 4 (Figs. 5.25a,b,d; Tables 5.1 & 5.11). Total work is significantly higher in Group 1 of Infant 3 (Fig. 5.25c; Table 5.1). This higher value of total work is due to her higher values of external work in Group 1 compared to Group 2 at a given velocity. Total work is significantly larger in Group 1 of the combined sample of infant baboons compared to Group 2 (Fig. 5.26; Table 5.3).

Total power requirements follow the same pattern as total work for between group analyses in this sample of infant baboons. Total power requirements do not differ significantly between groups for Infants 1,2 and 4 (Figs. 5.27a,b,d; Tables 5.1 & 5.12). Total power requirements are significantly higher in Group 1 of Infant 3 (Fig. 5.27c; Table 5.1). Total power is significantly larger in Group 1 of the combined sample of infant baboons compared to Group 2 (Fig. 5.28; Table 5.3).

Infants 1 - 3 do not show significant between group differences in total work when velocity was made dimensionless (Fig. 5.29a-c; Table 5.1). Infant 4 does

significantly less total work at its youngest age compared to its oldest age over the dimensionless velocity range (Fig. 5.29d; Table 5.13). The middle sampled age for Infant 4 does not differ significantly from the other groups (Fig. 5.29d; Table 5.13). Total work does not show significant between group differences in the combined sample of infant baboons over the dimensionless velocity range (Fig. 5.30; Table 5.3).

Total power requirements do not differ significantly between groups in any of the infant baboons at a given dimensionless velocity (Figs. 5.31a-d; Tables 5.1 & 5.14). Total power does not show significant between group differences in the combined sample of infant baboons over the dimensionless velocity range (Fig. 5.32; Table 5.3).

Comparison with other mammals

A comparison of work and power in the infant baboons to other mammals is made difficult by the fact that comparable data on internal, external and total power has only been reported for a single cursorial taxon, *Canis familiarus* from Fedak et al. (1982) and Heglund et al. (1982) and there are no comparable data on work reported for other mammalian quadrupeds. Comparisons reported here are therefore limited to infant baboons and the domestic dog from Fedak et al. (1982) and Heglund et al. (1982).

Because only least-squares regression equations relating internal, external, and total power in dogs have been reported, ANCOVA cannot be used. Therefore, the 95% confidence intervals of the regression lines for the infant baboon sample were calculated and significant differences were assumed when the regression line for the dog data set fell outside of this interval.

The infant baboon sample has lower internal power requirements compared to the dog sample (Fig. 5.33) from Fedak et al. (1982). These lower internal power requirements are consistent with the infant baboons' relatively lower stride frequencies compared to non-primate cursorial quadrupeds as demonstrated in Chapter 4.

The infant baboon sample has higher external power requirements compared to the dog sample (Fig. 5.34) from Heglund et al. (1982). Again these results are consistent with infant baboons' relatively longer strides compared to non-primate cursorial mammals (see Chapter 4).

Finally, the lower internal power requirements and the higher external power requirements in the infant baboons cancel each other out, and total power requirements are very similar in the infant baboon sample compared to the dog sample (Fig. 5.35). These data are consistent with the tradeoff mechanism described earlier.

Recovery of mechanical energy and gait

The percent of energy recovered through an exchange between potential and kinetic energy was examined in the infant baboon sample (see eq. 5.8). In all four infant baboons, the percent recovery of mechanical energy is high at low velocities and decreases with increasing velocity (Fig. 5.36). The infant baboons recover up to 74% of the mechanical energy used to lift and accelerate their centers of mass. These results are similar to those found for other mammalian quadrupeds (see Cavagna et al., 1977).

As described earlier, Reilly and Biknevicius (2003) suggest the interesting possibility that footfall sequence during walking may have an important effect on the ability to recover mechanical energy. The more closely forelimb and hindlimb footfalls

are coupled in time, the easier it is for an individual's four limbs to function as inverted pendula (Reilly and Biknevicius, 2003).

Footfall sequence appears to have no effect on the ability of the infant baboons to recover mechanical energy (Fig. 5.37). Percent recovery is mostly determined by velocity. Reilly and Biknevicius (2003) call attention to the possibility that single foot gaits (gait number ≈ 25 or 75) reduce an animal's ability to recover mechanical energy. These gaits represent a four-beat pattern where fore- and hindlimb touchdowns are evenly spaced in time (i.e. there is no fore/hindlimb coupling; see Chapter 1, Fig. 1.3). The infant baboons do not appear to have any problems recovering mechanical energy during single foot gaits (closed triangles in Fig. 5.37).

Reilly and Biknevicius (2003) also suggest that running mechanics are probably employed by animals during fast walking gaits (duty factors slightly greater than 50). These results were supported in a study of gray short-tailed opossums (*Monodelphis domestica*) by Parchman et al. (2003). The infant baboon sample does not, however support this hypothesis (Fig. 5.38). In fact, at duty factors near 50 (gray shaded area in Fig. 5.38), recoveries can be greater than 50%.

In most quadrupeds, the percent recovery falls to nearly zero in the middle range of velocities (trotting and running), and is still fairly low during galloping (see Cavagna et al., 1977). In this sample of infant baboons, there is no clear transition between walking, running, and galloping. Middle range running velocities can have percent recoveries over 30% (Figs. 5.36 & 5.38).

As noted earlier, primates, including these infant baboons, do not often use a true running trot with an aerial phase. The infant baboons mostly use an amble during

running velocities. An amble may occur at duty factors less than 50 when gait numbers are sufficiently different from 50 (a trot) that there is no whole body aerial phase (see Fig. 5.39).

The difference in kinetic and potential energy profiles in an amble and a true trot are shown in Figure 5.40. In an amble, when a hindlimb touches down, a forelimb is still on the ground and retracting, so it exerts a propulsive force on the body. This force should increase the forward kinetic energy of the body until the forelimb lifts off, and the braking force applied by the hindlimb dominates. Some exchange between potential and kinetic energy is therefore possible just after hindlimb touchdown in an amble. In a trot, however, when a hindlimb touches down, the ipsilateral forelimb has lifted off (the body was just aerial). So both kinetic and potential energy decrease at the same time. An amble will therefore redirect kinetic energy at key moments of the stride, allowing some amount of pendular exchange between potential and kinetic energy. This recovery may be essential to primates in general, who do not have the long tendons available for the storage and release of elastic strain energy. Evidence that the infant baboons do not use storage and recovery of strain energy is discussed below.

Elastic energy storage

The amount of energy that is stored and released by elastic mechanisms is notoriously difficult to calculate (see Cavagna et al., 1977; Heglund et al., 1982). The most accurate method is to measure muscle forces and length changes *in vivo* (see Roberts et al., 1997). In the absence of invasive techniques, it is possible to estimate whether or not elastic energy storage could play a role as an energy saving mechanism.

Cavagna et al. (1977) showed that the ratio of total mechanical power output ($\dot{W}_{tot}$) to metabolic energy input ($\dot{W}_{metab}$) can estimate the amount of elastic energy storage and recovery. This ratio is called the efficiency of positive work (γ ; Cavagna et al., 1977) or the apparent efficiency (Minetti et al., 1999) and is calculated after Cavagna et al. (1977) as:

$$\gamma = \frac{\dot{W}_{tot}}{\dot{W}_{metab}} \tag{5.12}$$

The maximum efficiency with which muscles can covert metabolic energy into mechanical energy is 0.25 (Cavagna et al., 1977; Woledge et al., 1985). If γ is greater than .25 then the difference must be explained by the storage and recovery of elastic energy (Cavagna et al., 1977). It is important to note that values of γ below .25 do not necessarily rule out the possibility of elastic storage, they simply suggest that it is less likely that the recovery of stored elastic energy plays an important role in the individual's locomotion (Cavagna et al., 1977).

$\dot{W}_{metab}$ was calculated for the infant baboons from the allometric equation in Taylor et al. (1982) for primates. This value may actually underestimate the true value of the rate of metabolic energy input since infant and juvenile individuals may have higher energy expenditures compared to adults of the same species (Steudel-Numbers, 2003). However in humans, correction for body mass effects on velocity using the Froude number eliminates this difference (see DeJaeger et al., 2001).

Efficiency in the infant baboons increases with increasing velocity (Fig. 5.41) as is the case in other quadrupedal mammals (Cavagna et al., 1977). These values do not,

however, rise above 0.25 until the highest velocities used by the infant baboon sample, and even then, it is only a small number of strides that fall above 0.25. The infant baboon sample has efficiencies lower than 0.25 at running velocities, indicating elastic energy storage and recovery is probably not an important part of their energy savings. In contrast to the infant baboons, horses, which are known to use elastic energy storage and recovery, have apparent efficiencies greater than .60 for most of their trotting velocities and over 1.0 when galloping (Minetti et al., 1999).

The lack of evidence for storage and recovery of elastic energy in the infant baboons is consistent with their continued use of pendular energy recovery mechanisms during running gaits. The use of these mechanisms may be adaptive in individuals who lack the long tendons in their distal limb segments necessary for the storage and recovery of elastic strain energy.

DISCUSSION

Work and power

Internal, external, and total work and power at similar raw velocities

This is the first study to examine ontogenetic changes in mechanical energy in a longitudinal sample of mammals. It is therefore somewhat difficult to place the results from this sample of infant baboons into the context of primate or non-primate mammalian patterns. As described earlier, Schepens et al. (2001; see also Heglund and Schepens, 2003; Schepens et al., 2004) have examined age-related changes in mechanical work and power in a cross-sectional sample of human children. Although they report

some intriguing possibilities for ascribing differences in metabolic energy demands to differences in mechanical work and power as the children age, when the effects of body size on velocity are taken into account using the Froude number, these differences disappear (Schepens et al., 2004).

It is important to take differences in body size into account. As shown in Chapter 4, differences in body size make analysis at the same absolute velocity somewhat meaningless because individuals of different sizes will "feel" the same velocity quite differently (at the same velocity, a horse may walk, a dog may trot, and a mouse may gallop). We should therefore expect that at different body sizes, mechanical work and power may differ between individuals simply because the effects of absolute velocities are influencing the individuals differently.

In this sample of infant baboons, individuals vary in their between-group differences in mechanical internal, external, and total work and power at similar absolute velocities. Some do show some signs of tradeoff mechanisms occurring. For example, Infant 1 had lower $\dot{W}_{int}$ and higher $\dot{W}_{ext}$ at younger ages, and these values canceled each other out so that $\dot{W}_{tot}$ never differed. The other individuals, however, do not show signs of ontogenetic tradeoff mechanisms over raw velocities.

Between group differences in work and power over raw velocities disappear for the most part when body size is taken into account through the use of dimensionless velocities. Only W_{int} and $\dot{W}_{int}$ differences for Infant 1 persist. For all other individuals, values of internal, external, and total work and power do not show significant between group differences.

Superficially, these data do not support the idea that differences in stride frequency and stride length among animals with different limb mass distributions will have opposite effects on W_{int} and W_{ext} (as well as $\dot{W}_{int}$ and $\dot{W}_{ext}$). It is possible, however, that the differences in stride frequency and length were too slight between groups of the infant baboons to elicit the diverging responses in internal and external energy outputs. Perhaps slight differences in spatio-temporal kinematics simply equalize energy outputs, rather than having the tradeoff effects described for humans in Cavagna and Franzetti (1986; see also Cavagna et al., 1991; Minetti and Saibene, 1992; Minetti et al., 1995).

Importantly, these results suggest that the effects of limb mass distribution on kinematics mitigates the possible negative effects of distal limb mass concentrations on W_{int} and $\dot{W}_{int}$. When body size is taken into account, the infant baboons do not use more W_{int} and $\dot{W}_{int}$ compared to older ages, despite differences in limb mass distributions.

Comparison to other mammals

The comparison of mechanical power in infant baboons and dogs provides a convincing case for the presence of a mechanical energy tradeoff mechanism. The infant baboons use lower stride frequencies and longer strides compared to cursorial mammals, including dogs (see Chapter 4). The infant baboons do less $\dot{W}_{int}$ and more $\dot{W}_{ext}$ compared to the dog sample. Their values of $\dot{W}_{tot}$ do not differ significantly from those of the dog sample. These results suggest that, contrary to Fedak et al. (1982) mass specific internal and external power may not be completely size independent. The tradeoff mechanism however, may render $\dot{W}_{tot}$ independent of body size. It is possible

that the trade-off mechanism is only apparent when stride frequencies and stride lengths differ greatly between taxa.

To explore the possibility that these tradeoffs may be occurring in other mammalian quadrupeds, $\dot{W}_{int}$ regression lines for the three quadrupeds in Fedak et al.'s (1982) data set were recalculated using the Froude number to adjust for differences in body size (Fig. 5.42). Values of $\dot{W}_{int}$ are similar in the horse and the dog, but are lower in the chipmunk. Dogs and horses are both cursorial quadrupeds, and so should use dynamically similar stride lengths and frequencies (see Alexander and Jayes, 1983). Chipmunks are non-cursorial quadrupeds, and as such, they should use relatively lower stride frequencies and longer strides compared to the more cursorial dog and horse (Alexander and Jayes, 1983). These results are consistent with the idea that kinematics may have strong effects on $\dot{W}_{int}$. Values of $\dot{W}_{ext}$ and $\dot{W}_{tot}$ could not be recalculated in this way because limb lengths were not provided for the other mammalian quadrupeds (see Heglund et al., 1982).

The force hypothesis

The existence of a mechanical work and power tradeoff mechanism supports the contention that all quadrupeds should do similar amounts of total work and power, independent of body size. Therefore, work and power should not explain the systematic decrease in costs of transport with increasing body mass noted by Taylor et al. (1982). Given the debate over the causes of energetic costs of locomotion in quadrupeds and bipeds, the infant baboons' kinematics are placed within the context of the force

hypothesis first articulated in full by Kram and Taylor (1990). Although controversial (see Heglund, 2004), this hypothesis gives one more possible reason why distal limb mass concentrations may not accrue a relatively higher energetic cost.

As described in Chapter 1, Kram and Taylor (1990) suggest that the metabolic cost of locomotion is dependent on the time over which forces must be developed by muscles and tendons to support body weight. If true, then metabolic costs would be determined mostly by the duration of stance phase (Kram and Taylor, 1990).

According to the force hypothesis, the long stance durations of large mammals allow the forces required to support body weight to accrue over a longer period of time, thereby reducing energetic costs. As shown in Chapter 4, distal limb mass concentrations not only increase swing durations, but also generally increase stance durations in the infant baboon sample. This result was a somewhat unexpected prediction of the locomotor model described in Chapter 3. If the infant baboons use similar, or even longer stance durations when their mass is most distal, then their costs may actually be lower.

Comparisons among animals of different size may be made by estimating the rate of increase in costs of locomotion with velocity (the cost of transport). Kram and Taylor (1990) suggest that the cost of transport should be related to step length. Mean step lengths were calculated at each age for the infant baboon sample. Weight specific costs of transport ($\frac{\dot{E}_{metab}}{W_b}$) were calculated according to the equation given in Kram and Taylor (1990) for the infant baboons at all sampled body masses:

$$\frac{\dot{E}_{metab}}{W_b} = c\frac{1}{L_1} \qquad (5.13)$$

where L_1 is step length (m), W_b is body weight (N) and c is the cost coefficient (.183 JN^{-1} for quadrupedal mammals).

The infant baboons fall below the regression line for other quadrupedal mammals (from Roberts et al., 1998) indicating lower net transport costs for these individuals (Fig. 5.43). These lower costs are a direct result of their longer step lengths compared to other quadrupedal mammals (Fig. 5.44), which in turn are caused by their relatively long stance durations (see Chapter 4).

Primates in general are expected to use relatively long step lengths (see Chapters 3 & 4; see also Larson et al., 2001). Is it then possible that primates have lower net costs of transport compared to other quadrupedal mammals? As discussed earlier, there are few data from which conclusions may be drawn. However, data from Taylor et al. (1982) indicate that quadrupedal primates in general appear to have lower net costs of transport compared to other mammals of similar size (see Fig. 5.45; note that these costs of transport are calculated as the slope of the cost of locomotion regression line). It is therefore possible that the long swing durations of primates that cause their long stance durations also lead to relatively low costs of transport for their body size.

This type of analysis may provide an explanation for the variability in costs of transport among similarly sized animals (see Taylor et al., 1982). If stance durations differ among these animals, then the variability in costs of transport may actually be due to differences in limb mass distribution patterns at a given body mass.

Energy saving mechanisms

Distal limb mass distributions do not appear to compromise infant baboons' ability to recover mechanical energy, especially during walking. But, an important energy saving mechanism that occurs during running gaits does not appear to play much of a role in the infant baboons. Calculations of energetic efficiencies in the infant sample indicate that they are probably not using elastic energy storage and recovery during running gaits. This result is not surprising given the results of Alexander et al. (1981) showing that primates' large distal limb muscles do not leave room for the long tendons necessary for storage and recovery of elastic strain energy (see also Preuschoft and Gunther, 1994).

Instead, the infant baboons make some use of pendular mechanics during running gaits. It is possible that the use of an amble during some of these runs allows for greater pendular transfers of energy than occurs during the trots and paces of non-primate quadrupeds. No other study has documented a degree of pendular energy recovery during gaits described as runs (Cavagna et al., 1977; Minetti et al., 1999; Parchman et al., 2003).

Schmitt et al. (2003) have shown that rather than trotting, primates in general appear to use the amble as their main running gait. The results from this study suggest that the use of the amble is a means by which primates may continue to use pendular energy saving mechanisms during running gaits. Elephants have also been shown to use the amble to attain high running velocities (Hutchinson et al., 2003). Alexander et al. (1981) demonstrated that elephants do not have the long distal segment tendons needed

for elastic energy recovery. It is therefore possible that elephants amble to make use of some degree of pendular energy recovery during running gaits.

Implications for primate evolution

The results from this study suggest that the evolution of grasping hands and feet in primates did not have to come at an energetic price. Because of their distal limb mass concentrations, primates adopt low stride frequencies and long strides, which most likely optimize their internal and external mechanical energy requirements, allowing them to maintain similar amounts of total mechanical work and power requirements compared to other quadrupeds. Additionally, their relatively long swing phases lead to relatively long stance phases. If the force hypothesis is correct, then these long stance phases may actually reduce their energy requirements compared to other quadrupeds of similar size.

The muscular adaptations for grasping hands and feet that appear to have reduced primates' abilities to make use of elastic storage and recovery of energy during running gaits do not compromise the energetic economy of their running gaits. Instead of using elastic mechanisms, primates may be employing pendular energy saving mechanisms in running gaits.

These results suggest that the locomotor kinematic characteristics of primates may be viewed from an energetic perspective as adaptations to compensate for primates' distal limb mass concentrations. Were it not for the energy saving mechanisms described above, the evolution of grasping hands and feet in the earliest primates would have been at the detriment of energetic costs of locomotion. That energetic costs were not associated with the evolution of grasping adaptations is a strong indication that the

reduction of energetic costs was a strong selective force in the evolution of primate locomotion.

Implications for the evolution of mammalian quadrupedalism

The results from this study may also explain why mammals of similar size, yet with drastically different limb mass distribution patterns, do not differ in their energetic costs. Specifically, Taylor et al. (1974) showed that the cheetah, the gazelle, and the goat do not differ in their energetic costs despite having different limb mass distributions. In Chapter 3, evidence was presented showing that domestic cats use relatively lower stride frequencies and longer strides than other mammalian cursors, and these low stride frequencies may be linked to their distal limb mass distributions. If cheetahs use similar kinematics compared to the domestic cats, then the use of low stride frequencies and long strides may explain their similar energetic costs compared to the goat and gazelle. Their low stride frequencies and long strides would reduce their internal energy outputs while increasing their external energy outputs, allowing them to maintain similar total energy outputs compared to other mammals.

It is possible that all mammals follow a similar tradeoff pattern that is dependent on their limb mass distributions. There would therefore be a combination of stride length and stride frequency at a given velocity, based on an individual's limb mass distribution that would allow all mammals to have similar total energy outputs. These results would explain the fact that all mammals studied to date have very similar total power outputs (Heglund et al., 1982).

If the force hypothesis correctly explains energetic costs in quadrupeds, then the results from this study may inform on the amount of variability in net costs of transport described by Taylor et al. (1982) and Heglund (1985). The variability may be related to differences in limb mass distributions among similarly sized taxa. Given two quadrupeds of the same size but with different limb mass distributions, the individual with more distal mass should use longer stance durations due to its longer swing durations. Therefore, its costs of transport should actually be *lower* than the individual with more proximal limb mass concentrations.

Summary and conclusions

Infant baboons do not differ significantly in the mechanical internal, external, or total energy outputs at a given dimensionless velocity regardless of limb mass distributions. Compared to dogs, the infant baboon sample has lower internal mechanical power outputs, higher external mechanical power outputs, and more similar total mechanical power outputs. These results suggest that, on a broad scale, individuals may use a combination of stride frequency and stride length that are determined by their limb mass distributions and that minimize total mechanical energy outputs.

Additionally, the infant baboons use pendular mechanics when running. This study is the first to document pendular energy savings during running in any taxon. It is likely that the use of this energy saving mechanism at high velocities is related to the fact that their distal limb mass concentrations do not allow them to have the long tendons in distal limb elements necessary to make use of storage and recovery of elastic energy as an energy saving mechanism during running.

These findings suggest that non-cursorial selection pressures acting on the distal limb elements of primates, and perhaps other mammals in general, do not have to exact an energetic price. Quadrupeds may adjust their kinematics to accommodate limb mass distribution patterns that, superficially, seem detrimental to quadrupedal energetics.

Overall, the results from this study highlight the importance of energetic considerations in the evolution of quadrupedal kinematics. The intensity of energetics as a selection pressure remains to be determined, yet the impacts of selection acting on kinematics to maintain reasonable energy expenditures are apparent and must be taken into account in our understanding of the evolution of primate and non-primate quadrupedalism.

TABLES

Table 5.1. LSMeans and 95% confidence intervals for between group comparisons of all work and power variables with both velocity and dimensionless velocity as covariates in Infants 1-3.

Variable	***Covariate***	***Group***	***LSMean***	***95% CI***	***H_0:LSMean1 =LSMean2***
W_{int}	Velocity	Infant 1 Group 1	-1.357	-0.048	**<.0001**
W_{int}	Velocity	Infant 1 Group 2	-1.145	-0.031	
W_{int}	Velocity	Infant 2 Group 1	-0.917	0.045	0.463
W_{int}	Velocity	Infant 2 Group 2	-0.898	0.022	
W_{int}	Velocity	Infant 3 Group 1	-0.947	0.034	**0.001**
W_{int}	Velocity	Infant 3 Group 2	-1.015	0.014	
W_{ext}	Velocity	Infant 1 Group 1	-0.461	0.106	0.554
W_{ext}	Velocity	Infant 1 Group 2	-0.423	0.066	
W_{ext}	Velocity	Infant 2 Group 1	-0.291	0.042	0.618
W_{ext}	Velocity	Infant 2 Group 2	-0.279	0.021	
W_{ext}	Velocity	Infant 3 Group 1	-0.302	0.050	**<.0001**
W_{ext}	Velocity	Infant 3 Group 2	-0.414	0.020	
W_{tot}	Velocity	Infant 1 Group 1	-0.464	0.111	0.254
W_{tot}	Velocity	Infant 1 Group 2	-0.389	0.069	
W_{tot}	Velocity	Infant 2 Group 1	-0.192	0.037	0.595
W_{tot}	Velocity	Infant 2 Group 2	-0.181	0.019	
W_{tot}	Velocity	Infant 3 Group 1	-0.210	0.042	**<.0001**
W_{tot}	Velocity	Infant 3 Group 2	-0.314	0.017	

Variable	*Covariate*	*Group*	*LSMean*	*95% CI*	*H_0:LSMean1= LSMean2*
$\dot{W}_{int}$	Velocity	Infant 1 Group 1	-1.168	0.046	**<.0001**
$\dot{W}_{int}$	Velocity	Infant 1 Group 2	-0.974	0.030	
$\dot{W}_{int}$	Velocity	Infant 2 Group 1	-0.698	0.049	0.529
$\dot{W}_{int}$	Velocity	Infant 2 Group 2	-0.715	0.025	
$\dot{W}_{int}$	Velocity	Infant 3 Group 1	-0.770	0.036	**<.0001**
$\dot{W}_{int}$	Velocity	Infant 3 Group 2	-0.874	0.014	
$\dot{W}_{ext}$	Velocity	Infant 1 Group 1	-0.220	0.071	**0.025**
$\dot{W}_{ext}$	Velocity	Infant 1 Group 2	-0.316	0.043	
$\dot{W}_{ext}$	Velocity	Infant 2 Group 1	-0.072	0.041	0.292
$\dot{W}_{ext}$	Velocity	Infant 2 Group 2	-0.096	0.020	
$\dot{W}_{ext}$	Velocity	Infant 3 Group 1	-0.125	0.046	**<.0001**
$\dot{W}_{ext}$	Velocity	Infant 3 Group 2	-0.273	0.018	
$\dot{W}_{tot}$	Velocity	Infant 1 Group 1	-0.171	0.078	0.557
$\dot{W}_{tot}$	Velocity	Infant 1 Group 2	-0.197	0.046	
$\dot{W}_{tot}$	Velocity	Infant 2 Group 1	0.027	0.037	0.233
$\dot{W}_{tot}$	Velocity	Infant 2 Group 2	0.002	0.018	
$\dot{W}_{tot}$	Velocity	Infant 3 Group 1	-0.129	0.047	**<.0001**
$\dot{W}_{tot}$	Velocity	Infant 3 Group 2	-0.286	0.019	
W_{int}	Dimensionless Velocity	Infant 1 Group 1	-1.369	0.115	**<.0001**
W_{int}	Dimensionless Velocity	Infant 1 Group 2	-1.054	0.072	
W_{int}	Dimensionless Velocity	Infant 2 Group 1	-0.941	0.043	0.339

Variable	*Covariate*	*Group*	*LSMean*	*95% CI*	*H_0:LSMean1= LSMean2*
W_{int}	Dimensionless Velocity	Infant 2 Group 2	-0.890	0.022	
W_{int}	Dimensionless Velocity	Infant 3 Group 1	-1.026	0.038	0.183
W_{int}	Dimensionless Velocity	Infant 3 Group 2	-0.999	0.013	
W_{ext}	Dimensionless Velocity	Infant 1 Group 1	-0.477	0.106	0.337
W_{ext}	Dimensionless Velocity	Infant 1 Group 2	-0.416	0.066	
W_{ext}	Dimensionless Velocity	Infant 2 Group 1	-0.304	0.041	0.165
W_{ext}	Dimensionless Velocity	Infant 2 Group 2	-0.271	0.021	
W_{ext}	Dimensionless Velocity	Infant 3 Group 1	-0.388	0.056	0.738
W_{ext}	Dimensionless Velocity	Infant 3 Group 2	-0.398	0.020	
W_{tot}	Dimensionless Velocity	Infant 1 Group 1	-0.480	0.112	0.130
W_{tot}	Dimensionless Velocity	Infant 1 Group 2	-0.379	0.070	
W_{tot}	Dimensionless Velocity	Infant 2 Group 1	-0.208	0.036	0.099
W_{tot}	Dimensionless Velocity	Infant 2 Group 2	-0.173	0.019	
W_{tot}	Dimensionless Velocity	Infant 3 Group 1	-0.296	0.047	0.950
W_{tot}	Dimensionless Velocity	Infant 3 Group 2	-0.297	0.017	
$\dot{W}_{int}$	Dimensionless Velocity	Infant 1 Group 1	-1.195	0.114	**<.0001**
$\dot{W}_{int}$	Dimensionless Velocity	Infant 1 Group 2	-0.873	0.071	
$\dot{W}_{int}$	Dimensionless Velocity	Infant 2 Group 1	-0.735	0.047	0.234
$\dot{W}_{int}$	Dimensionless Velocity	Infant 2 Group 2	-0.703	0.024	
$\dot{W}_{int}$	Dimensionless Velocity	Infant 3 Group 1	-0.822	0.037	0.076

Variable	*Covariate*	*Group*	*LSMean*	*95% CI*	*H_0:LSMean1= LSMean2*
$\dot{W}_{int}$	Dimensionless Velocity	Infant 3 Group 2	-0.864	0.014	
$\dot{W}_{ext}$	Dimensionless Velocity	Infant 1 Group 1	-0.304	0.105	0.269
$\dot{W}_{ext}$	Dimensionless Velocity	Infant 1 Group 2	-0.235	0.065	
$\dot{W}_{ext}$	Dimensionless Velocity	Infant 2 Group 1	-0.098	0.039	0.531
$\dot{W}_{ext}$	Dimensionless Velocity	Infant 2 Group 2	-0.084	0.020	
$\dot{W}_{ext}$	Dimensionless Velocity	Infant 3 Group 1	-0.259	0.051	0.745
$\dot{W}_{ext}$	Dimensionless Velocity	Infant 3 Group 2	-0.250	0.018	
$\dot{W}_{tot}$	Dimensionless Velocity	Infant 1 Group 1	-0.307	0.109	0.094
$\dot{W}_{tot}$	Dimensionless Velocity	Infant 1 Group 2	-0.197	0.068	
$\dot{W}_{tot}$	Dimensionless Velocity	Infant 2 Group 1	-0.002	0.036	0.444
$\dot{W}_{tot}$	Dimensionless Velocity	Infant 2 Group 2	0.014	0.018	
$\dot{W}_{tot}$	Dimensionless Velocity	Infant 3 Group 1	-0.261	0.051	0.947
$\dot{W}_{tot}$	Dimensionless Velocity	Infant 3 Group 2	-0.262	0.018	

Table 5.2. LSMeans and 95% confidence intervals for between group comparisons of W_{int} in Infant 4 with velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.363	**0.020**	-1.308	0.147
2	-	0.080	-1.225	0.107
3		-	-1.116	0.058

Table 5.3. LSMeans and 95% confidence intervals of between group comparisons of all work and power variables with both velocity and dimensionless velocity as the covariates in the combined sample of infant baboons (Infants 1-3).

Variable	Covariate	LSmean1	CI	LSmean2	CI	H_0:LSMean1= LSMean2
W_{int}	velocity	-0.997	0.022	-0.992	0.011	0.685
$\dot{W}_{int}$	velocity	-0.820	0.015	-0.840	0.015	0.237
W_{ext}	velocity	-0.289	0.030	-0.373	0.015	**<.0001**
$\dot{W}_{ext}$	velocity	-0.104	0.029	-0.223	0.015	**<.0001**
W_{tot}	velocity	-0.207	0.025	-0.275	0.013	**<.0001**
$\dot{W}_{tot}$	velocity	-0.054	0.032	-0.176	0.016	**<.0001**
W_{int}	Dimensionless velocity	-1.067	0.021	-0.972	0.011	**<.0001**
$\dot{W}_{int}$	Dimensionless velocity	-0.923	0.022	-0.811	0.011	**<.0001**
W_{ext}	Dimensionless velocity	-0.347	0.029	-0.354	0.015	0.650
$\dot{W}_{ext}$	Dimensionless velocity	-0.203	0.028	-0.194	0.015	0.594
W_{tot}	Dimensionless velocity	-0.267	0.024	-0.256	0.013	0.435
$\dot{W}_{tot}$	Dimensionless velocity	-0.151	0.031	-0.145	0.016	0.741

Table 5.4. LSMeans and 95% confidence intervals for between group comparisons of $\dot{W}_{int}$ in Infant 4 with velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.811	0.390	-1.209	0.156
2	-	0.446	-1.186	0.114
3		-	-1.137	0.062

Table 5.5. LSMeans and 95% confidence intervals for between group comparisons of W_{int} in Infant 4 with dimensionless velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.303	**0.006**	-1.321	0.129
2	-	**0.042**	-1.236	0.102
3		-	-1.117	0.052

Table 5.6. LSMeans and 95% confidence intervals for between group comparisons of $\dot{W}_{int}$ in Infant 4 with dimensionless velocity as the covariate.

Grouping	2	3	LSmean	95% CI
1	0.615	0.160	-1.230	0.130
2	-	0.317	-1.189	0.103
3		-	-1.131	0.052

Table 5.7. LSMeans and 95% confidence intervals for between group comparisons of W_{ext} in Infant 4 with velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.361	0.070	-0.647	0.264
2	-	0.303	-0.498	0.193
3		-	-0.385	0.105

Table 5.8. LSMeans and 95% confidence intervals for between group comparisons of $\dot{W}_{ext}$ in Infant 4 with velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.576	0.308	-0.548	0.260
2	-	0.619	-0.459	0.189
3		-	-0.406	0.103

Table 5.9. LSMeans and 95% confidence intervals for between group comparisons of W_{ext} in Infant 4 with dimensionless velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.385	0.057	-0.641	0.242
2	-	0.265	-0.507	0.191
3		-	-0.388	0.097

Table 5.10. LSMeans and 95% confidence intervals for between group comparisons of $\dot{W}_{ext}$ in Infant 4 with dimensionless velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.533	0.230	-0.550	0.228
2	-	0.565	-0.460	0.180
3		-	-0.402	0.091

Table 5.11. LSMeans and 95% confidence intervals for between group comparisons of W_{tot} in Infant 4 with velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.333	0.051	-0.564	0.238
2	-	0.251	-0.422	0.173
3		-	-0.309	0.094

Table 5.12. LSMeans and 95% confidence intervals for between group comparisons of $\dot{W}_{tot}$ in Infant 4 with velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.567	0.281	-0.465	0.235
2	-	0.579	-0.383	0.171
3		-	-0.330	0.093

Table 5.13. LSMeans and 95% confidence intervals for between group comparisons of W_{tot} in Infant 4 with dimensionless velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.343	**0.036**	-0.561	0.216
2	-	0.211	-0.431	0.171
3		-	-0.311	0.087

Table 5.14. LSMeans and 95% confidence intervals for between group comparisons of $\dot{W}_{tot}$ in Infant 4 with dimensionless velocity as the covariate.

Grouping	2	3	LS mean	95% CI
1	0.499	0.186	-0.470	0.202
2	-	0.514	-0.384	0.160
3		-	-0.326	0.081

FIGURES

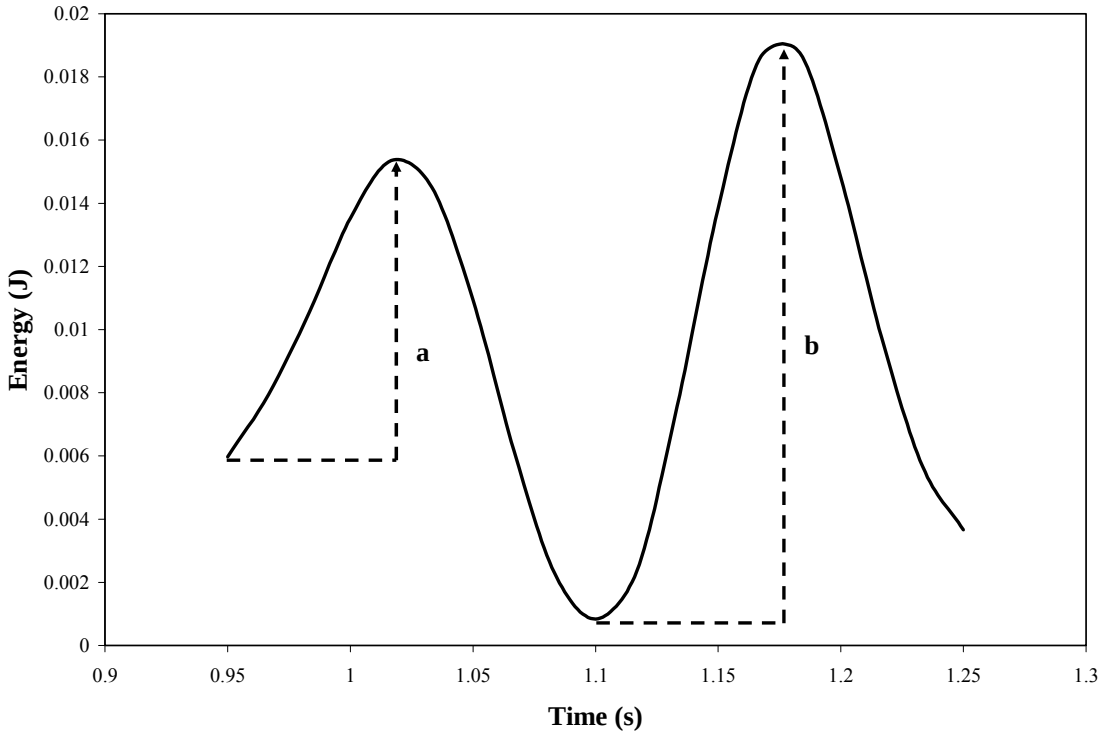


Figure 5.1. Method for calculating the positive changes in segmental energy.

Measurement of the positive changes in a segment's energy over an entire stride is calculated as the difference between a minimum in a segment's energy curve and the next maximum (a or b). These values are summed over an entire stride for all segments.

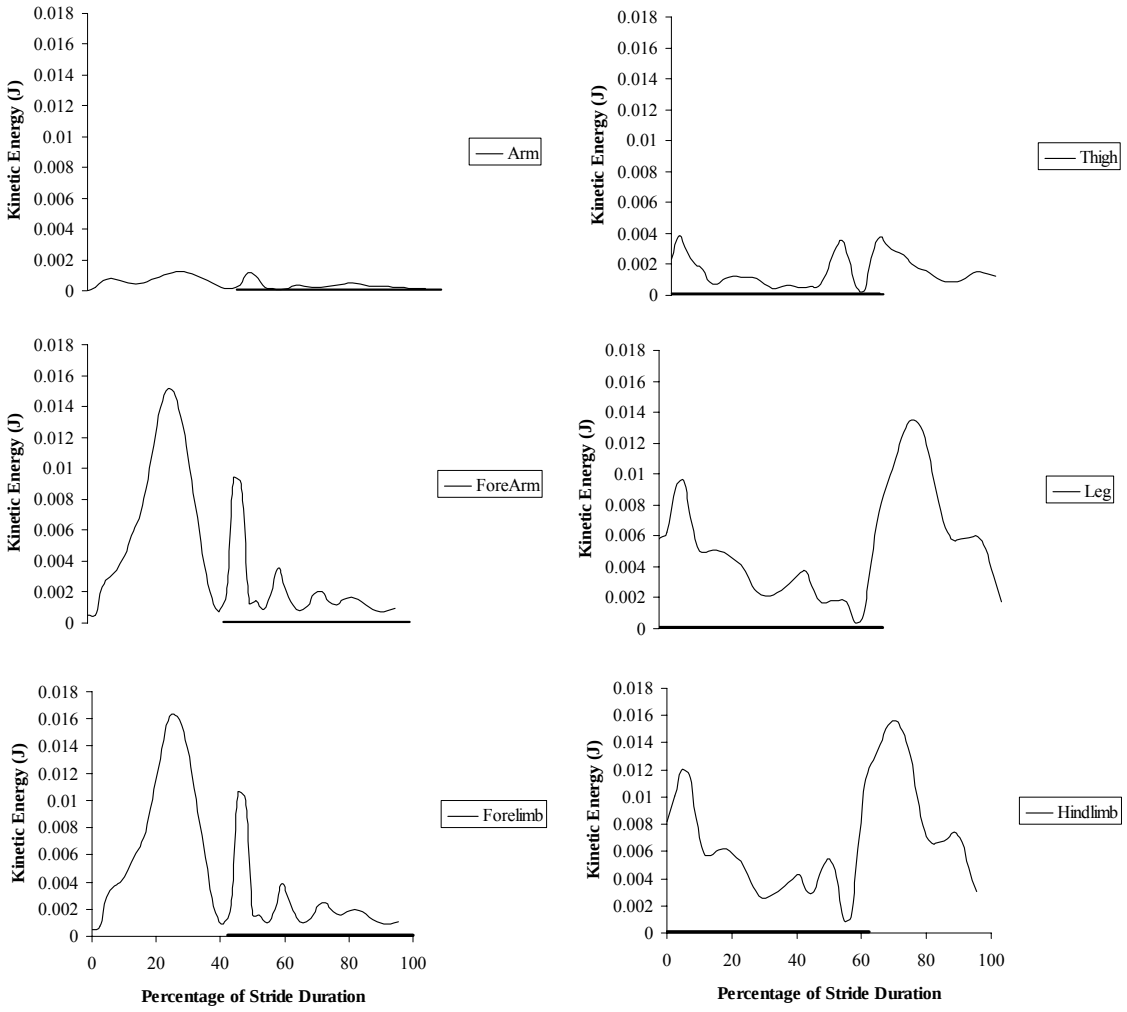


Figure 5.2. Segment and whole limb instantaneous kinetic energy for one infant baboon at a walking velocity (v=.50 m/s).

Forelimb and forelimb segment energy profiles are shown on the left, hindlimb and hindlimb segment energy profiles are shown on the right. Thick bars on the x-axis represent time of ground contact for the given limb (stance duration). See text for further details. Note the peak kinetic energy for either limb does not rise above 0.017 J.

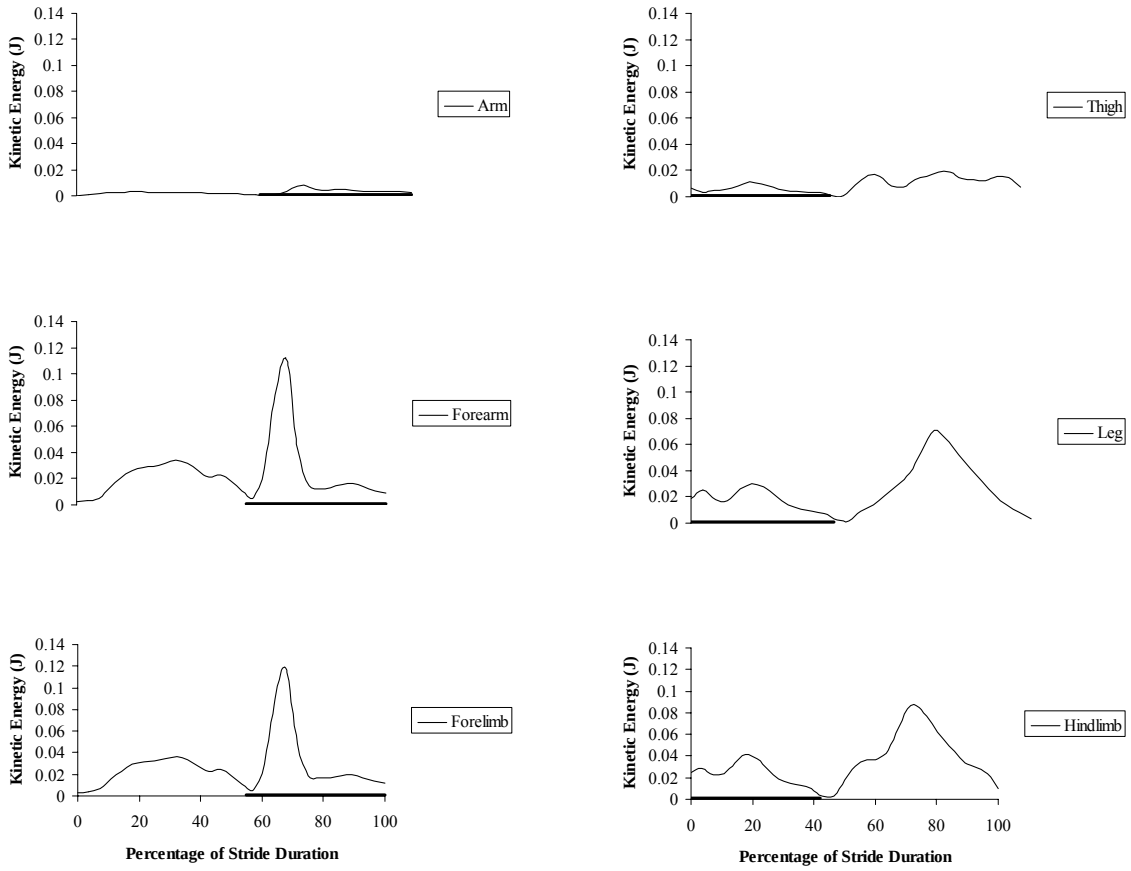


Figure 5.3. Segment and whole limb instantaneous kinetic energy for one infant baboon at a running velocity (v=1.14 m/s).

Forelimb and forelimb segment energy profiles are shown on the left, hindlimb and hindlimb segment energy profiles are shown on the right. Thick bars on the x-axis represent time of ground contact for the given limb (stance duration). See text for further details. Note that the peak forelimb (0.12 J) and hindlimb (0.10 J) kinetic energy is higher than at the walking velocity.

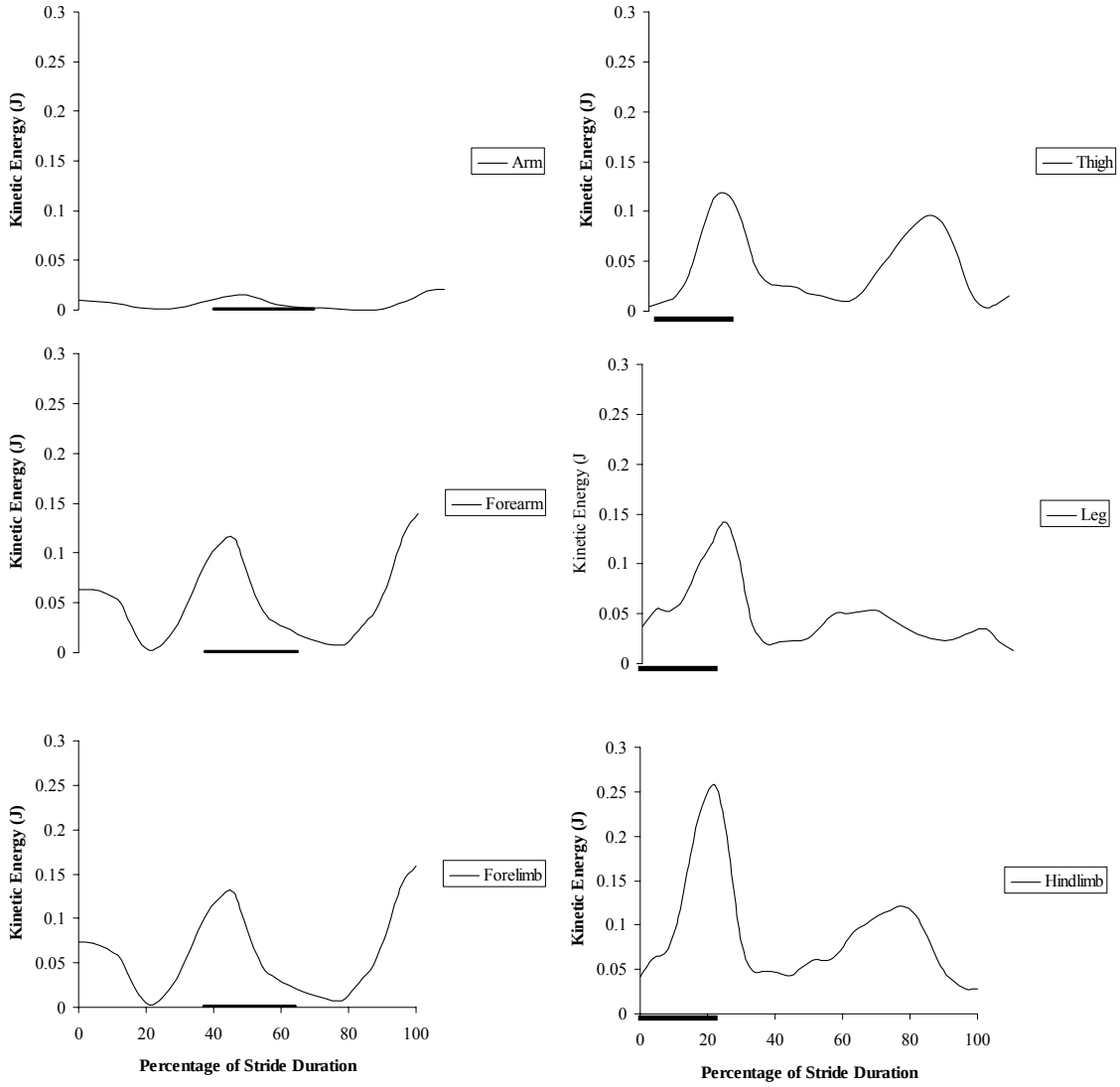


Figure 5.4. Segment and whole limb instantaneous kinetic energy for one infant baboon at a galloping velocity (v=2.4 m/s).

Forelimb and forelimb segment energy profiles are shown on the left, hindlimb and hindlimb segment energy profiles are shown on the right. Thick bars on the x-axis represent time of ground contact for the given limb (stance duration). See text for further details. Note that the peak limb kinetic energies are higher than at the running velocity.

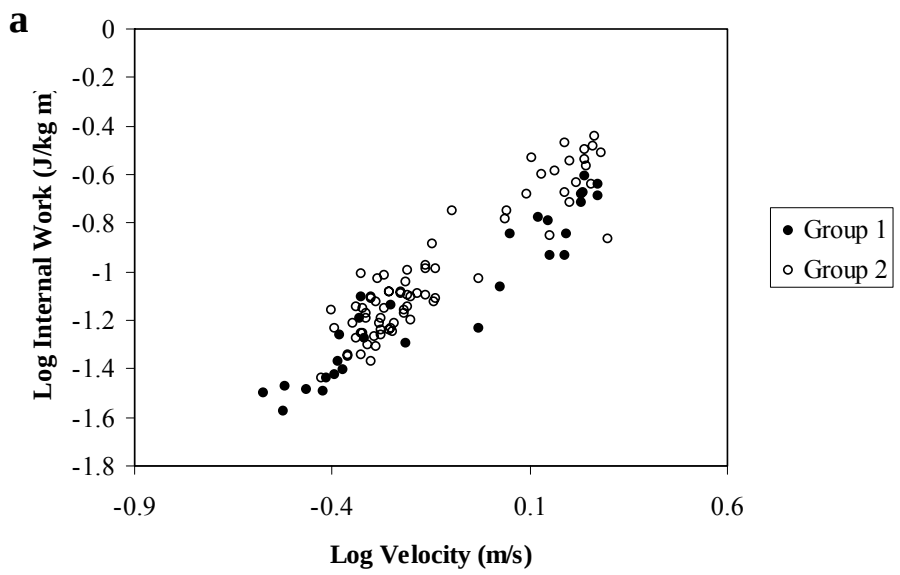


Figure 5.5a. Relationship between mass-specific internal work and velocity in Infant 1.

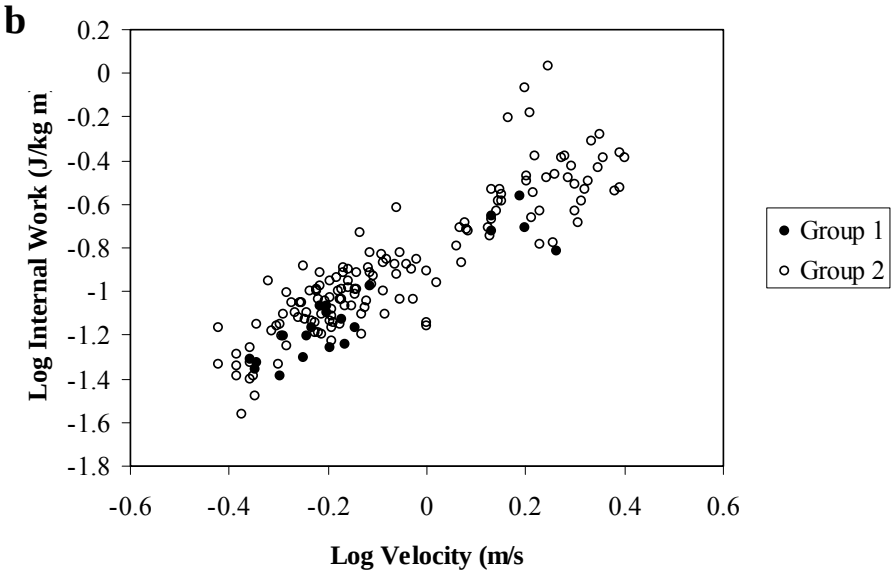


Figure 5.5b. Relationship between mass-specific internal work and velocity in Infant 2.

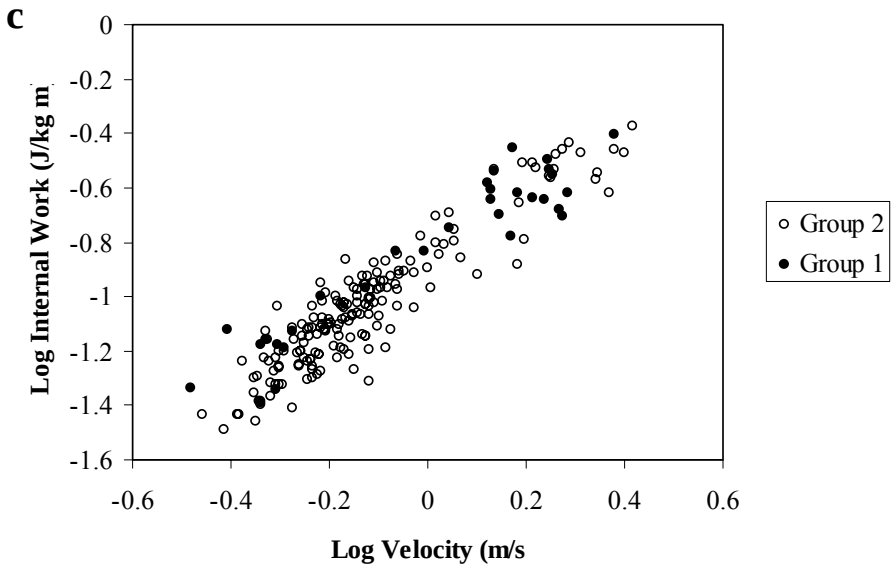


Figure 5.5c. Relationship between mass-specific internal work and velocity in Infant 3.

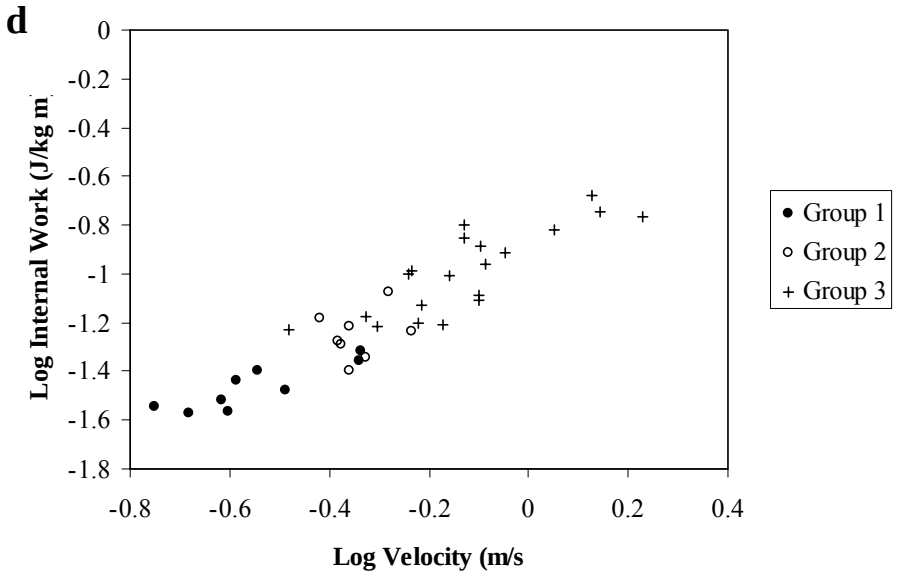


Figure 5.5d. Relationship between mass-specific internal work and velocity in Infant 4.

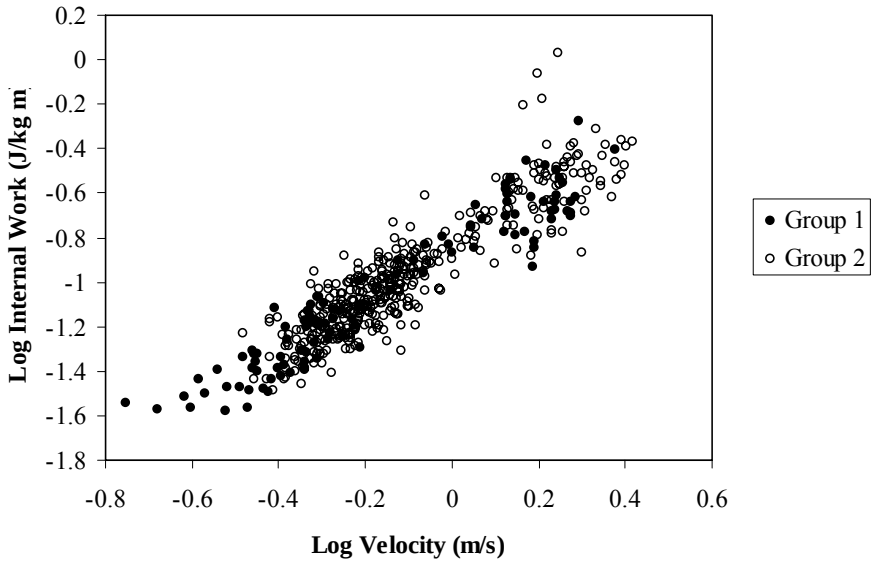


Figure 5.6. Mass-specific internal work in the combined infant baboon sample.

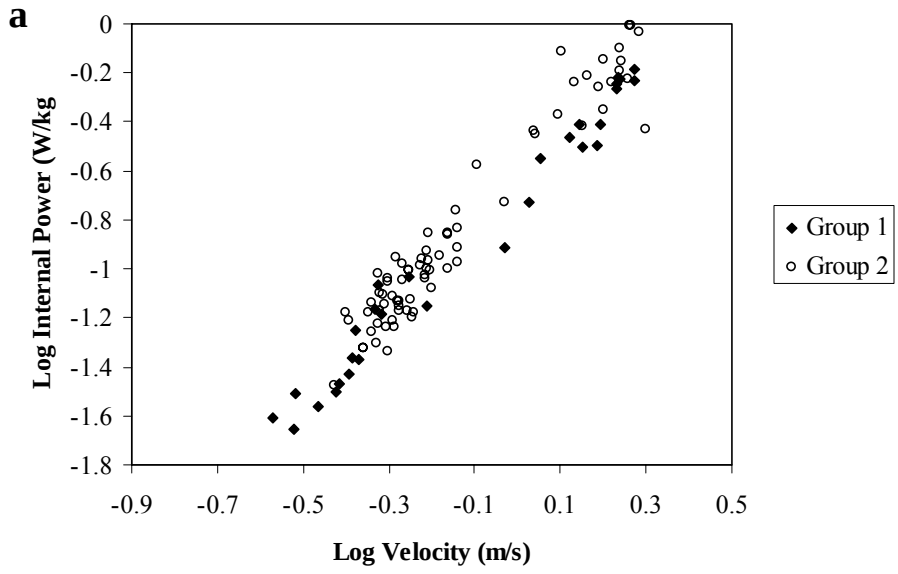


Figure 5.7a. Mass-specific internal power in Infant 1.

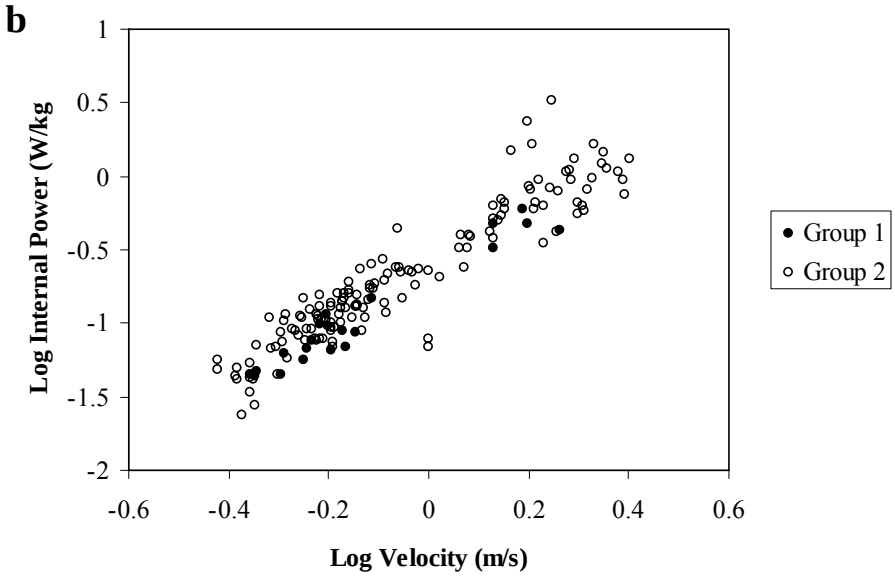


Figure 5.7b. Mass-specific internal power in Infant 2.

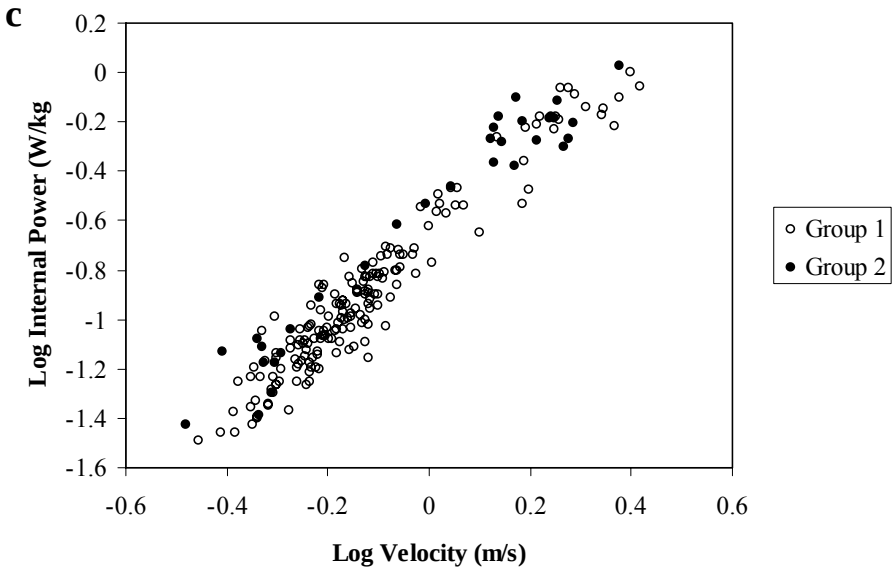


Figure 5.7c. Mass-specific internal power in Infant 3.

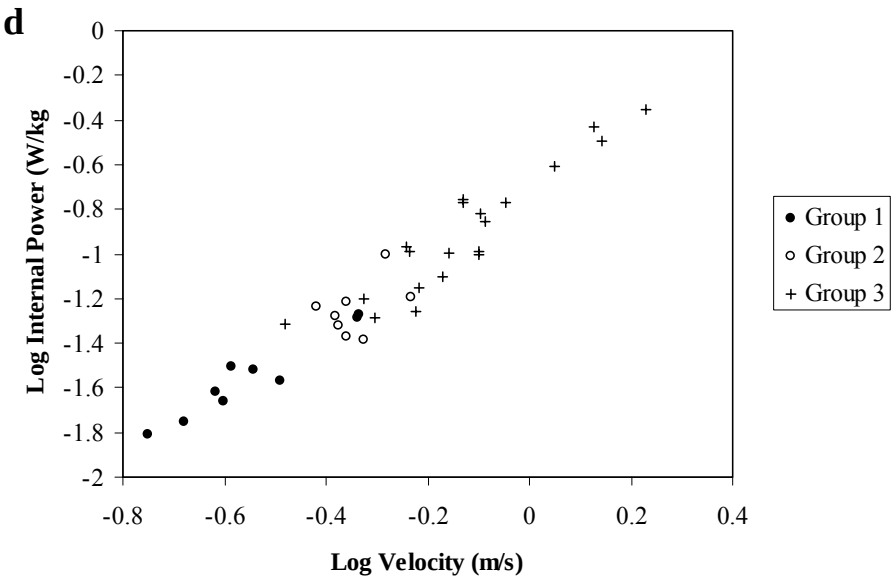


Figure 5.7d. Mass-specific internal power in Infant 4.

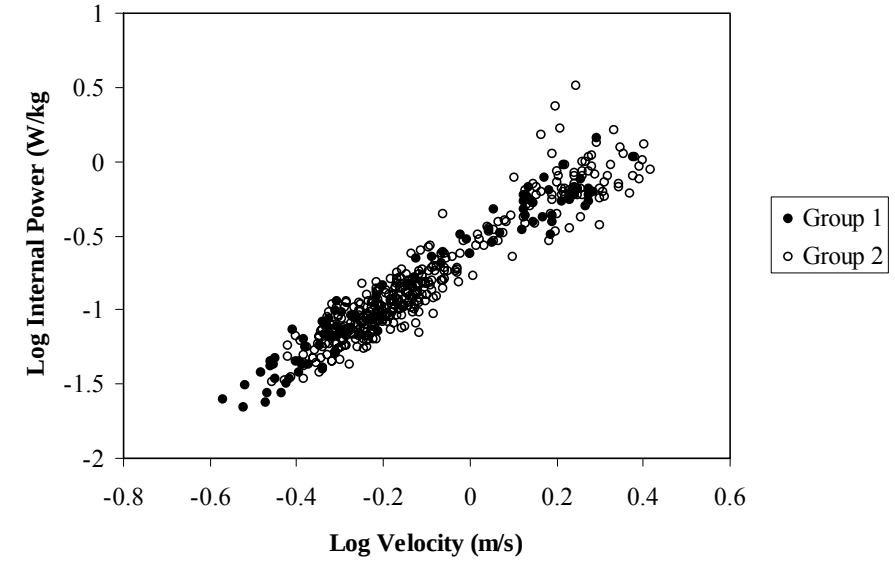


Figure 5.8. Mass-specific internal power in the combined infant sample.

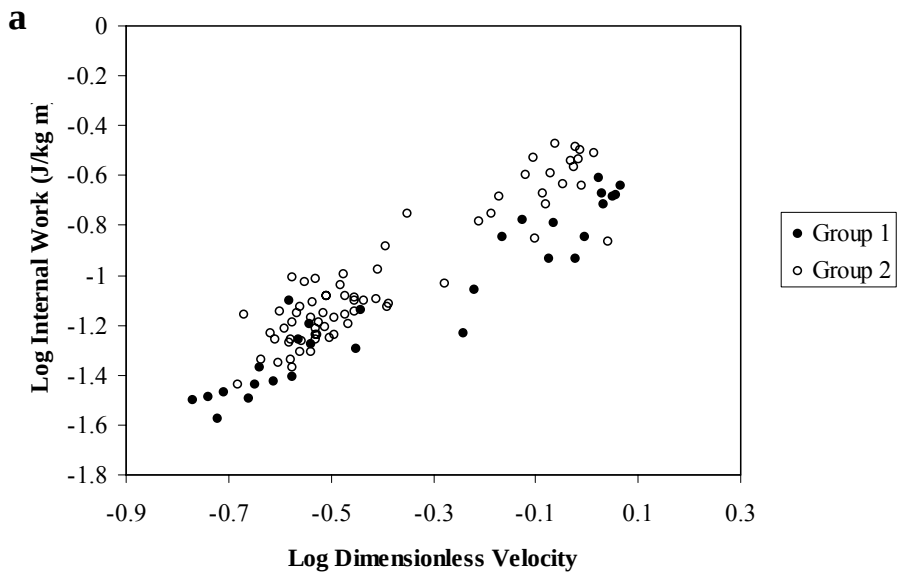


Figure 5.9a. Mass-specific internal power in Infant 1 over the dimensionless velocity range.

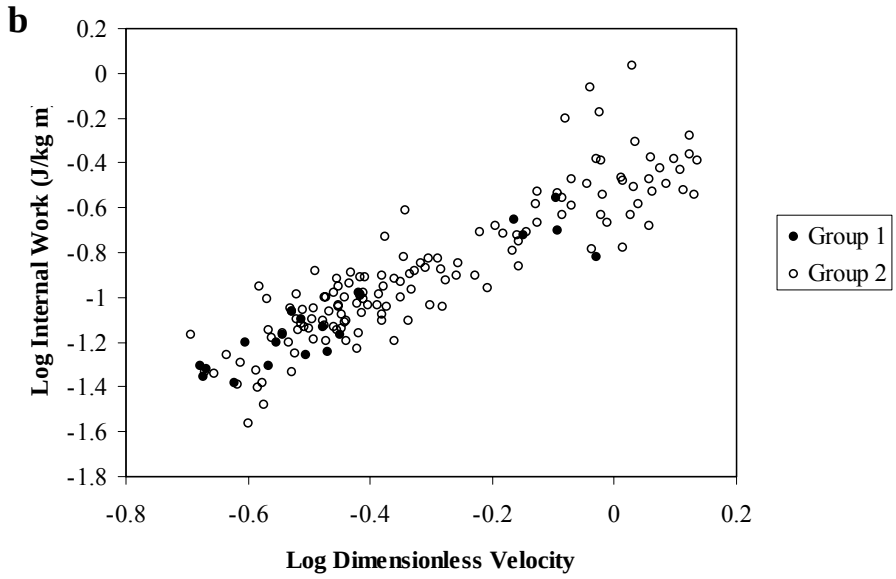


Figure 5.9b. Mass-specific internal power in Infant 2 over the dimensionless velocity range.

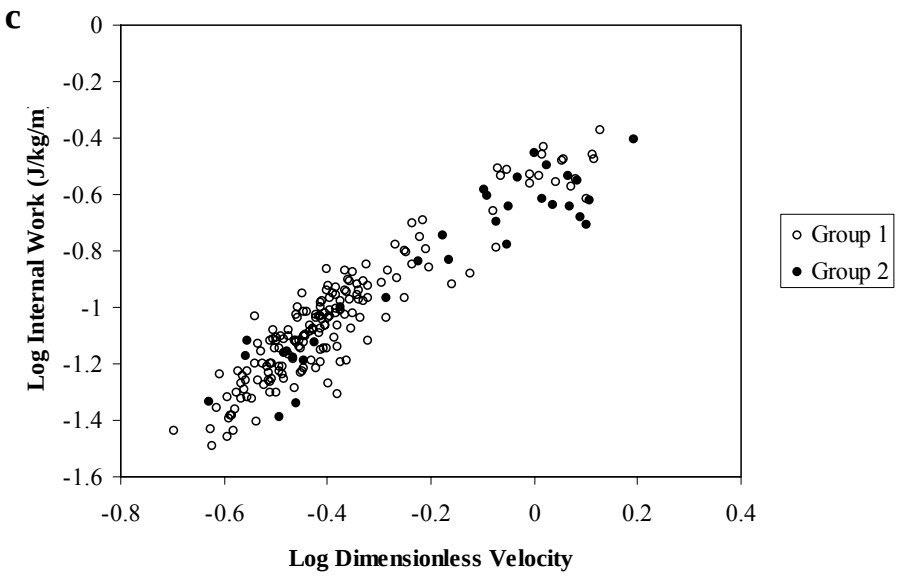


Figure 5.9c. Mass-specific internal power in Infant 3 over the dimensionless velocity range.

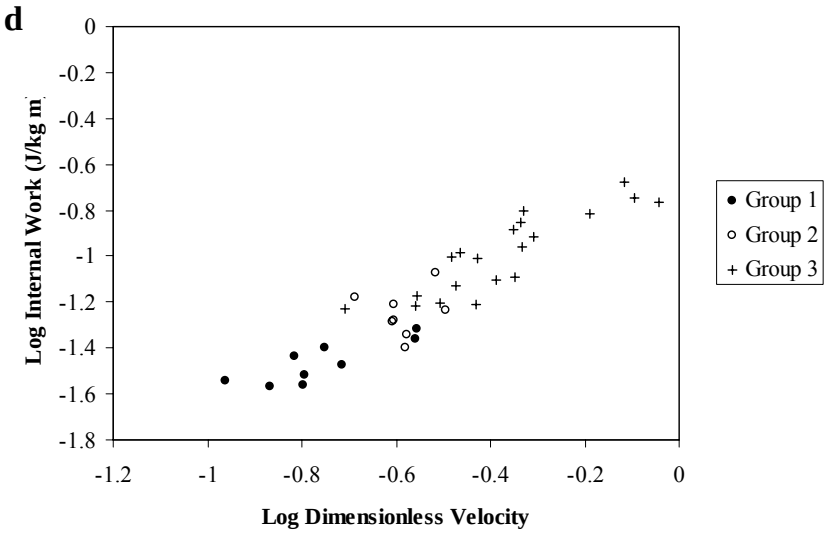


Figure 5.9d. Mass-specific internal power in Infant 4 over the dimensionless velocity range.

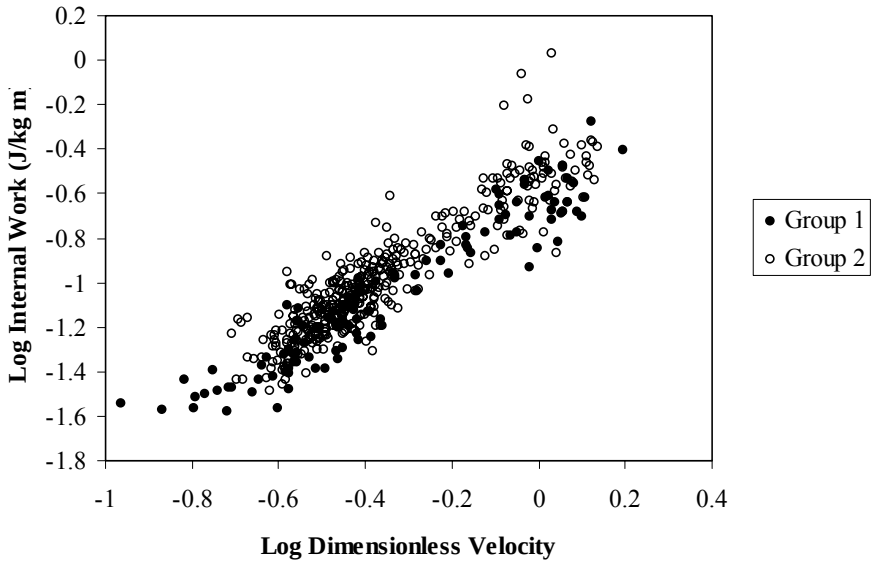


Figure 5.10. Mass-specific internal power in combined infant baboon sample.

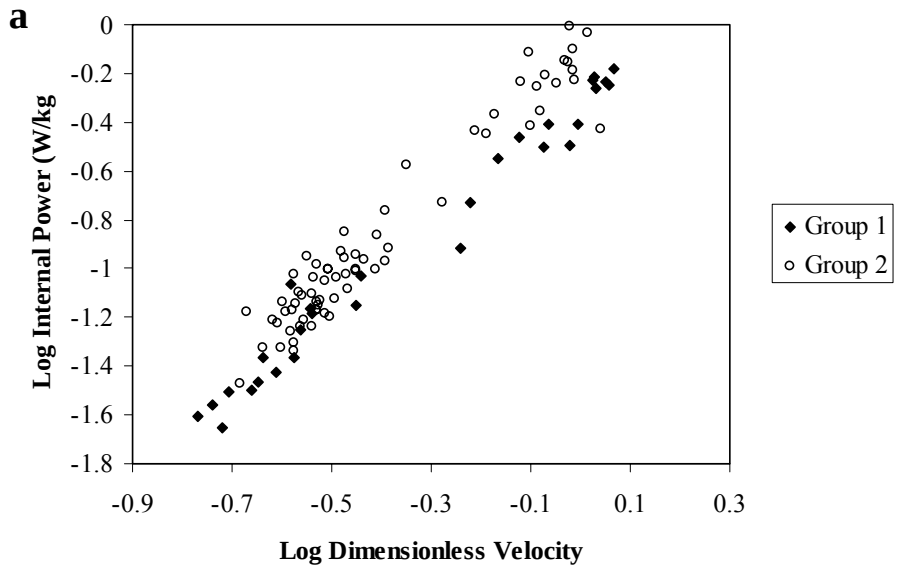


Figure 5.11a. Mass-specific internal power in Infant 1 over the dimensionless velocity range.

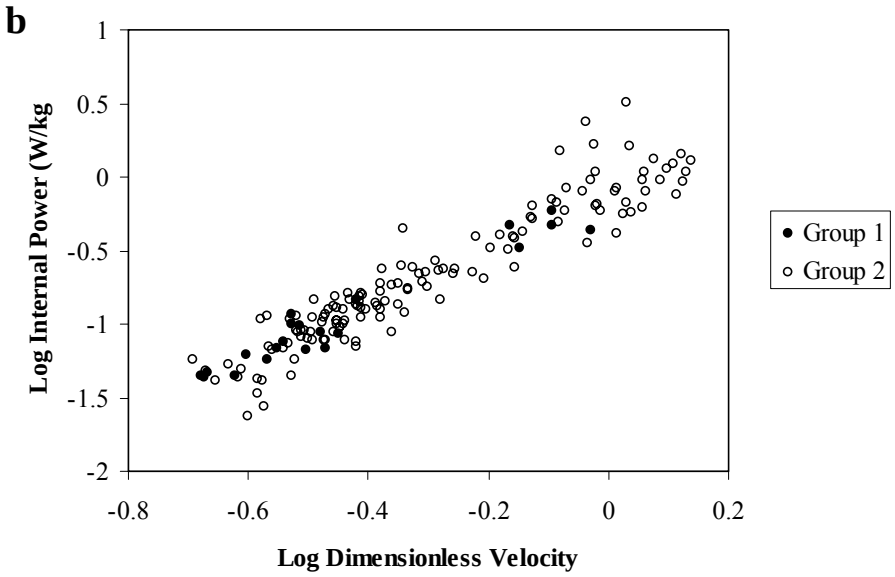


Figure 5.11b. Mass-specific internal power in Infant 2.

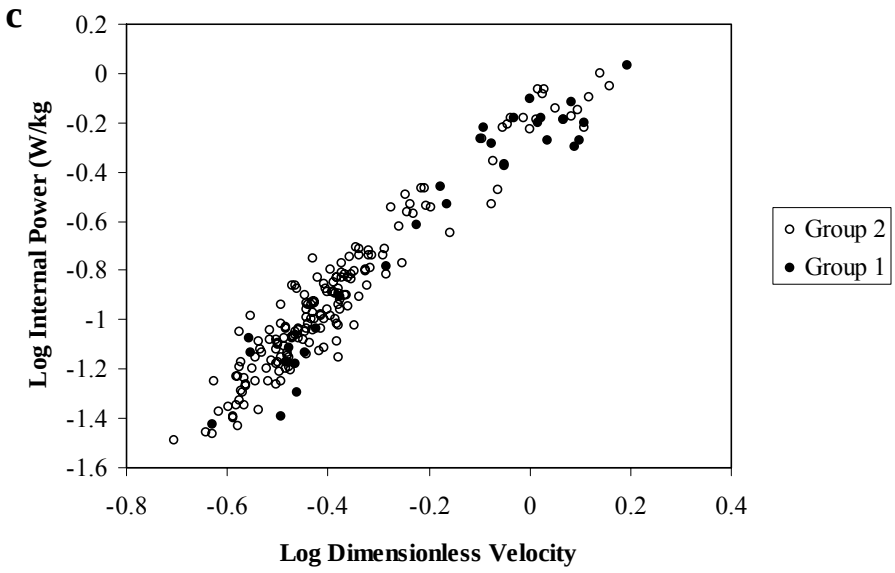


Figure 5.11c. Mass-specific internal power in Infant 3.

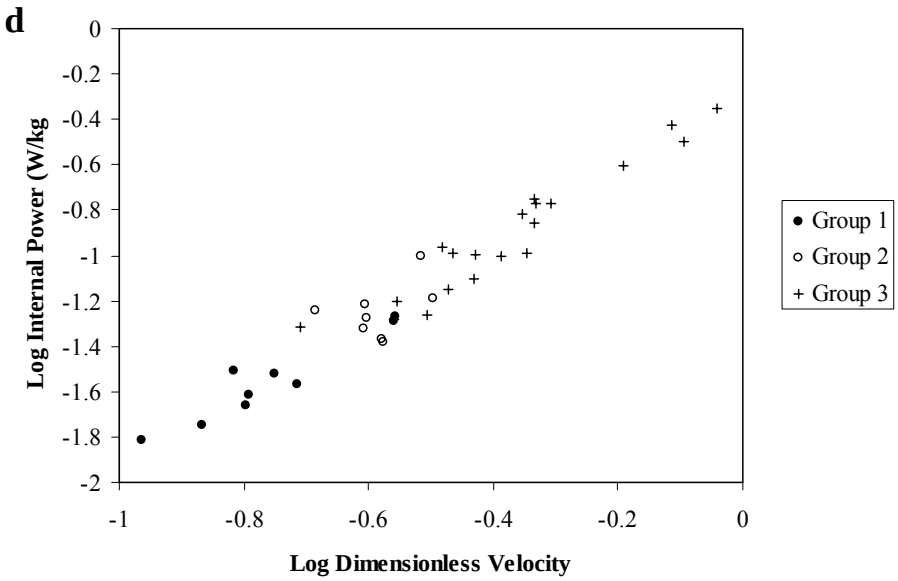


Figure 5.11d. Mass-specific internal power in Infant 4.

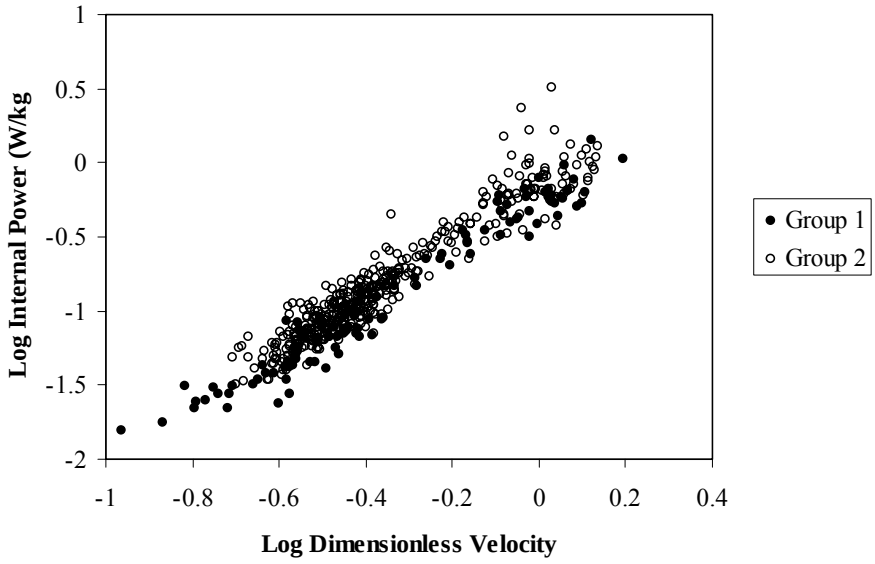


Figure 5.12. Mass-specific internal power in the combined sample of infant baboons.

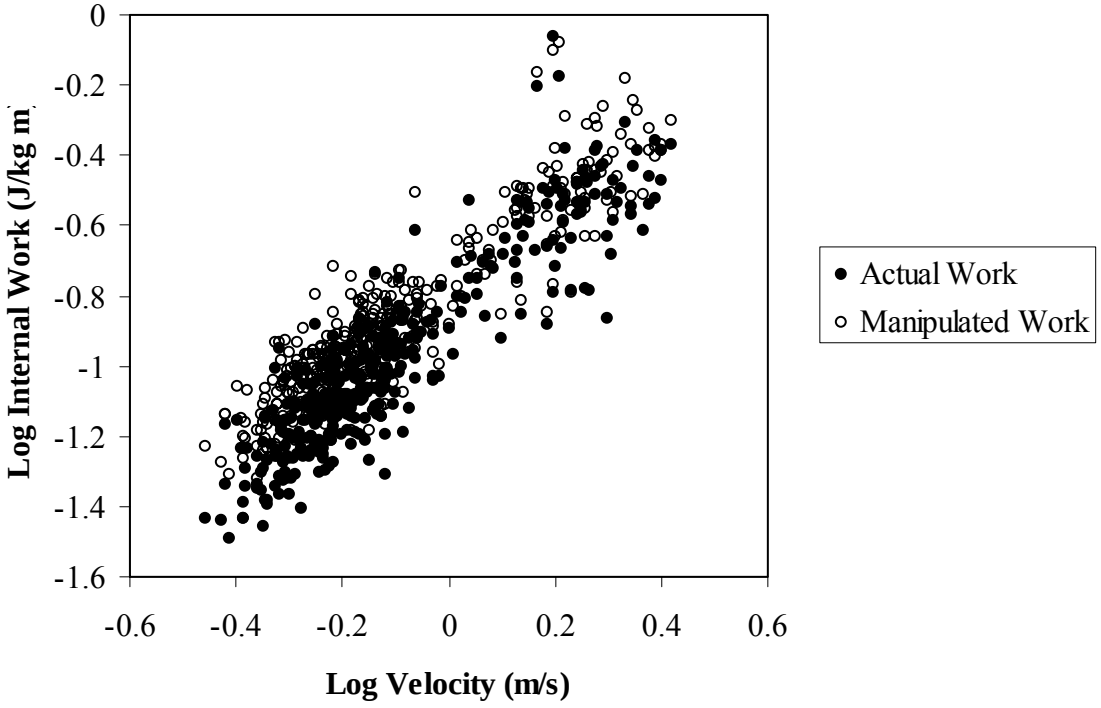


Figure 5.13. Effects of manipulations in limb inertial properties on mass-specific internal work.

Limb inertial properties in all Group 2 individuals were scaled to the inertial properties of Infant 2 at age 1.97 months. Infant 2 at age 1.97 months had the most distal limb mass distribution pattern of all sampled infants. Mass-specific internal work increased by an average of 20% in the manipulated sample.

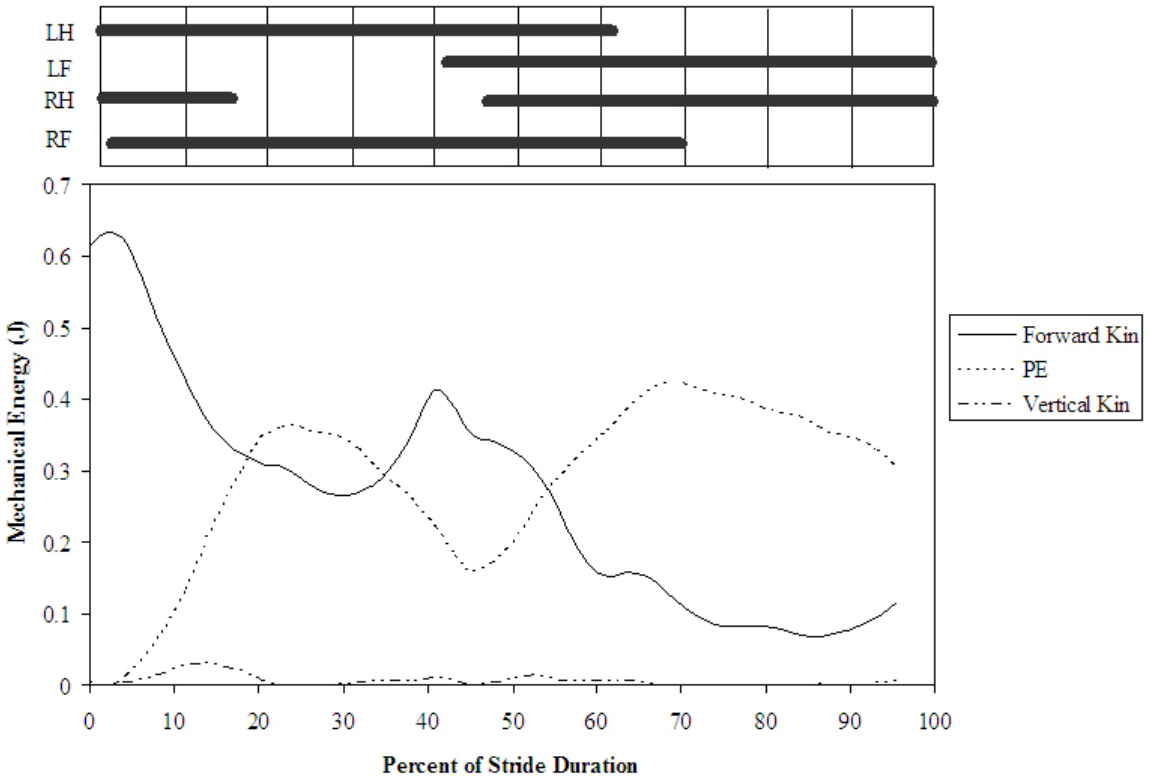


Figure 5.14. Energy Changes of the center of mass for an individual infant baboon at a walking speed. Potential (dotted line) and vertical kinetic (dot-dashed line) energy changes of the center of mass are basically in phase with each other. Forward kinetic energy (solid line) is 180 degrees out of phase allowing for a pendular exchange of energy. A footfall diagram for this stride is presented above the figure. Stance durations of the left hindlimb (LH), left forelimb (LF), right hindlimb (RH), and right forelimb (RF) are represented by solid bars. Vertical lines are the percentage of the stride and correspond to the x-axis of the center of mass energy change figure. Contralateral fore- and hindlimb touchdowns are closely coupled in time. After the LH and RF touchdown, potential energy and vertical kinetic energy rises and forward kinetic energy falls. After mid-stance for the LH and RF, potential energy and vertical kinetic energy decrease as forward kinetic energy increases.

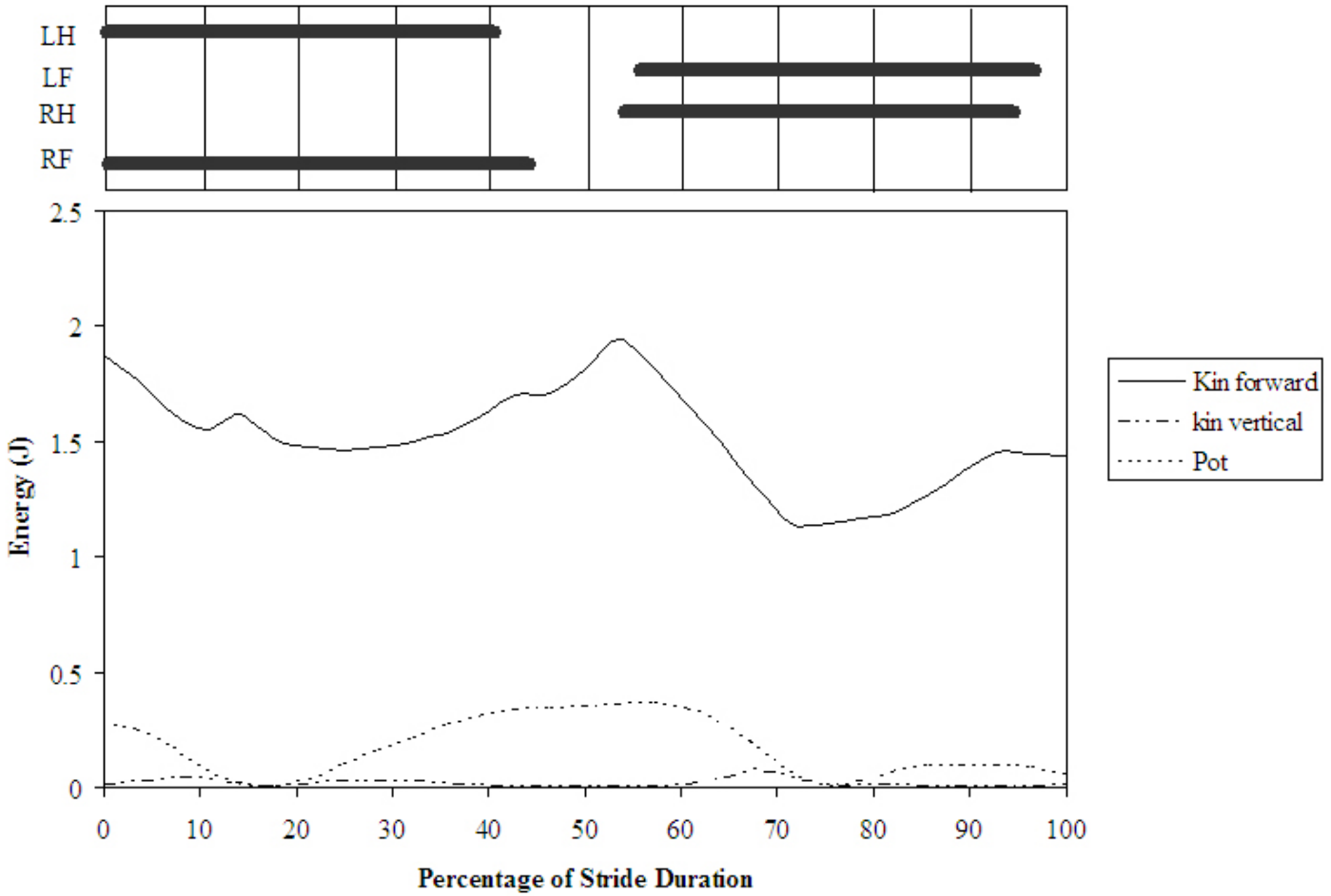


Figure 5.15. Energy changes of the center of mass for an individual infant baboon at a trotting speed. Gait diagram and symbols same as Figure 5.14. In a trot, when the contralateral fore- and hindlimbs (LH and RF) touchdown potential, vertical kinetic, and forward kinetic fall in phase. After mid-stance, these energy values rise, in phase until the next contralateral fore- and hindlimbs touchdown. There is little possibility of energy exchange in trotting because of the in phase relationship between potential and kinetic energy.

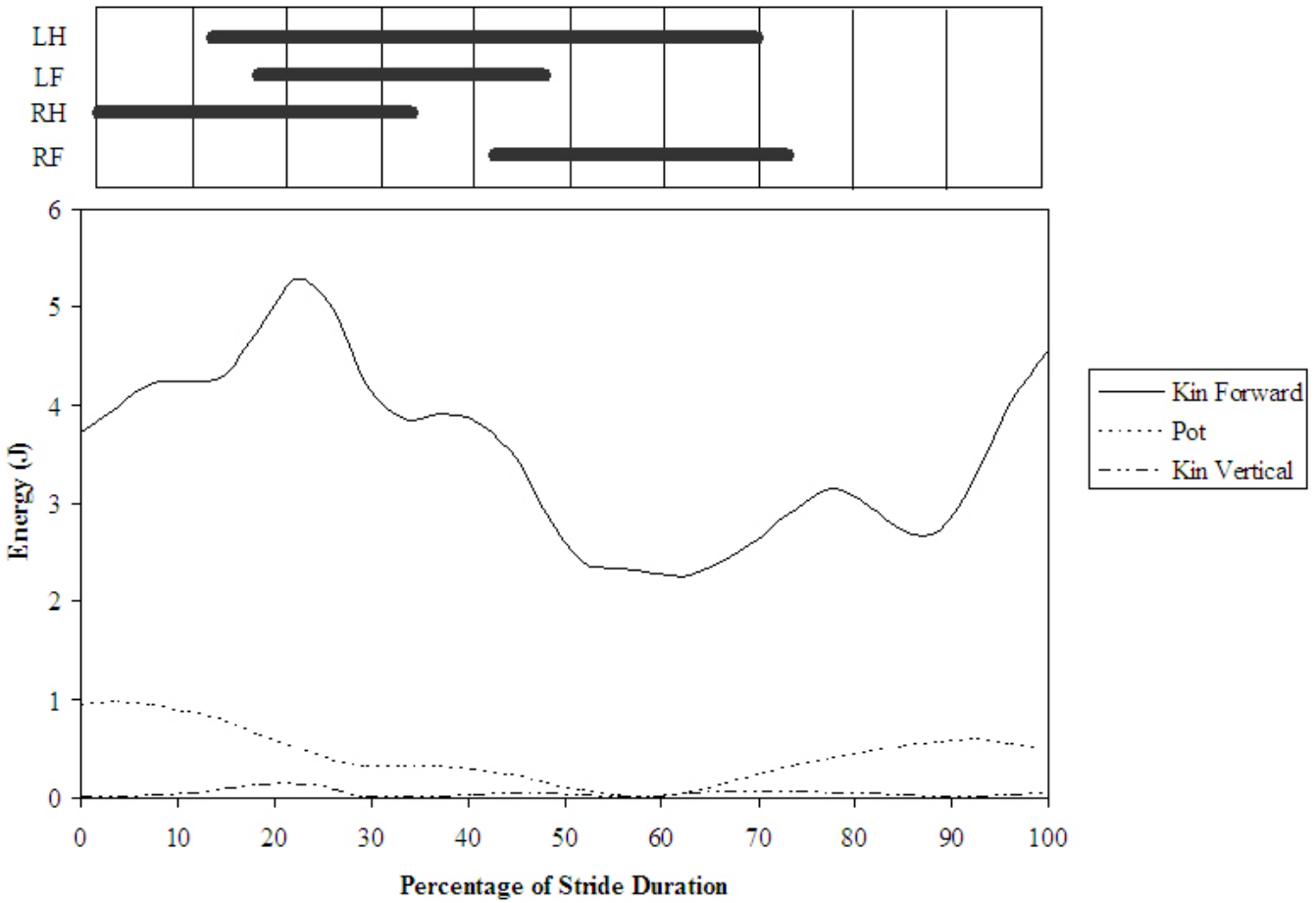


Figure 5.16. Energy changes of the center of mass for an individual infant baboon at a galloping speed. Gait diagram and symbols same as 5.14. In a gallop, there is the possibility of both some pendular exchange of energy and some elastic energy storage and recovery. After RH and LH touchdown, potential energy decreases and kinetic energy increases, allowing for some exchange. After RH lifts-off and RF touches down, potential and kinetic energy both drop in phase. At this time of the stride, tendons may be stretched, storing elastic energy. This energy is recovered after mid-stance of the forelimb, as potential and kinetic energy rise in phase.

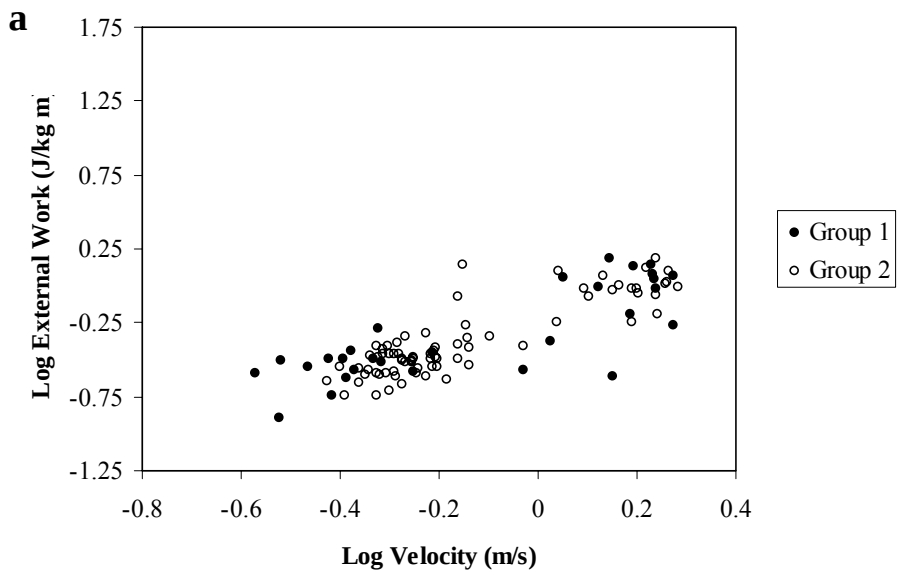


Figure 5.17a. External work in Infant 1.

External work is compared between Group 1 and Group 2 in Infant 1 over the raw velocity range. External work does not significantly differ between groups for Infant 1.

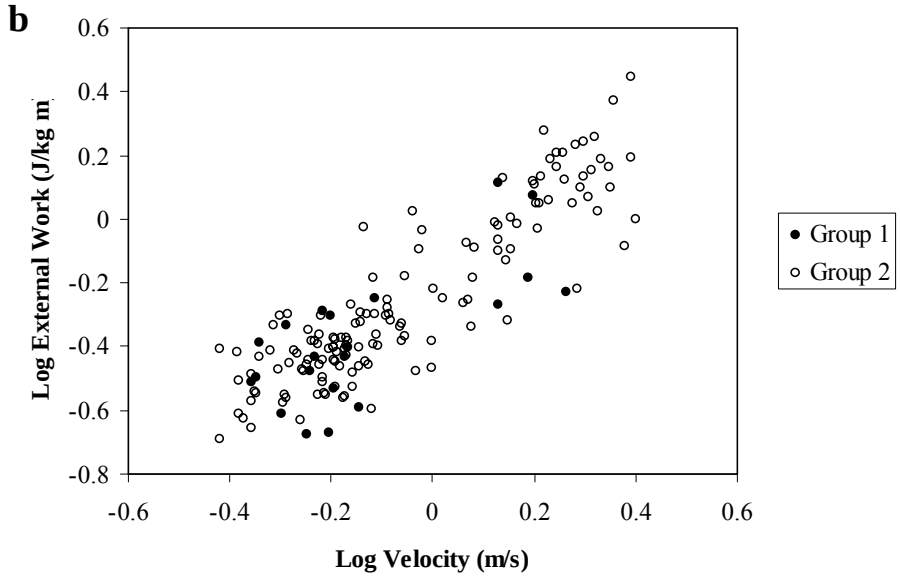


Figure 5.17b. External work in Infant 2.

External work is compared between Group 1 and Group 2 in Infant 2 over the raw velocity range. External work does not significantly differ between groups for Infant 2.

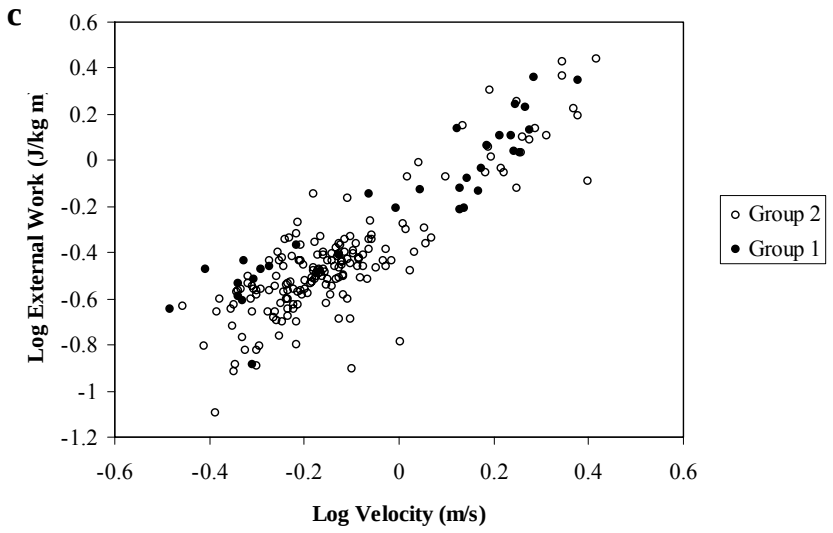


Figure 5.17c. External work in Infant 3.

External work is compared between Group 1 and Group 2 in Infant 3 over the raw velocity range. External work is significantly higher in Group 1 compared to Group 2. This difference occurs at slow speeds only. At higher speeds, external work values are similar between groups.

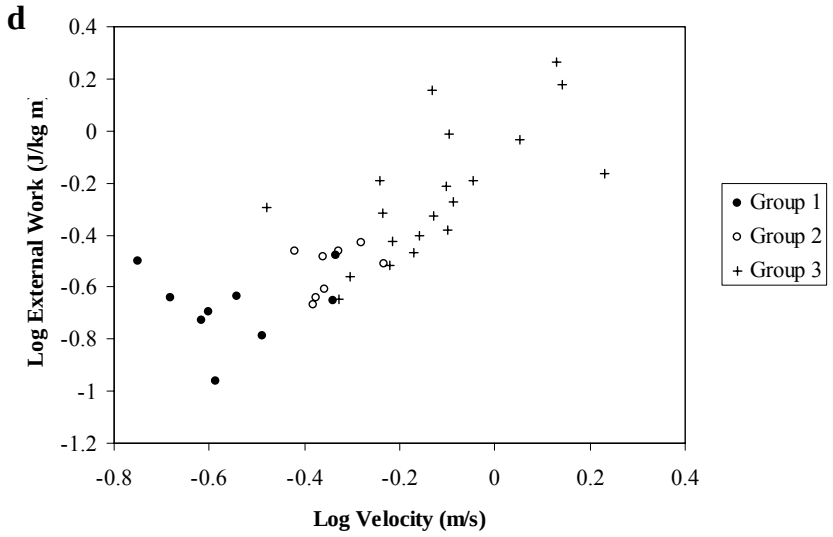


Figure 5.17d. External work in Infant 4.

External work is compared between Group 1 and Group 2 in Infant 4 over the raw velocity range. External work does not significantly differ between groups for Infant 4.

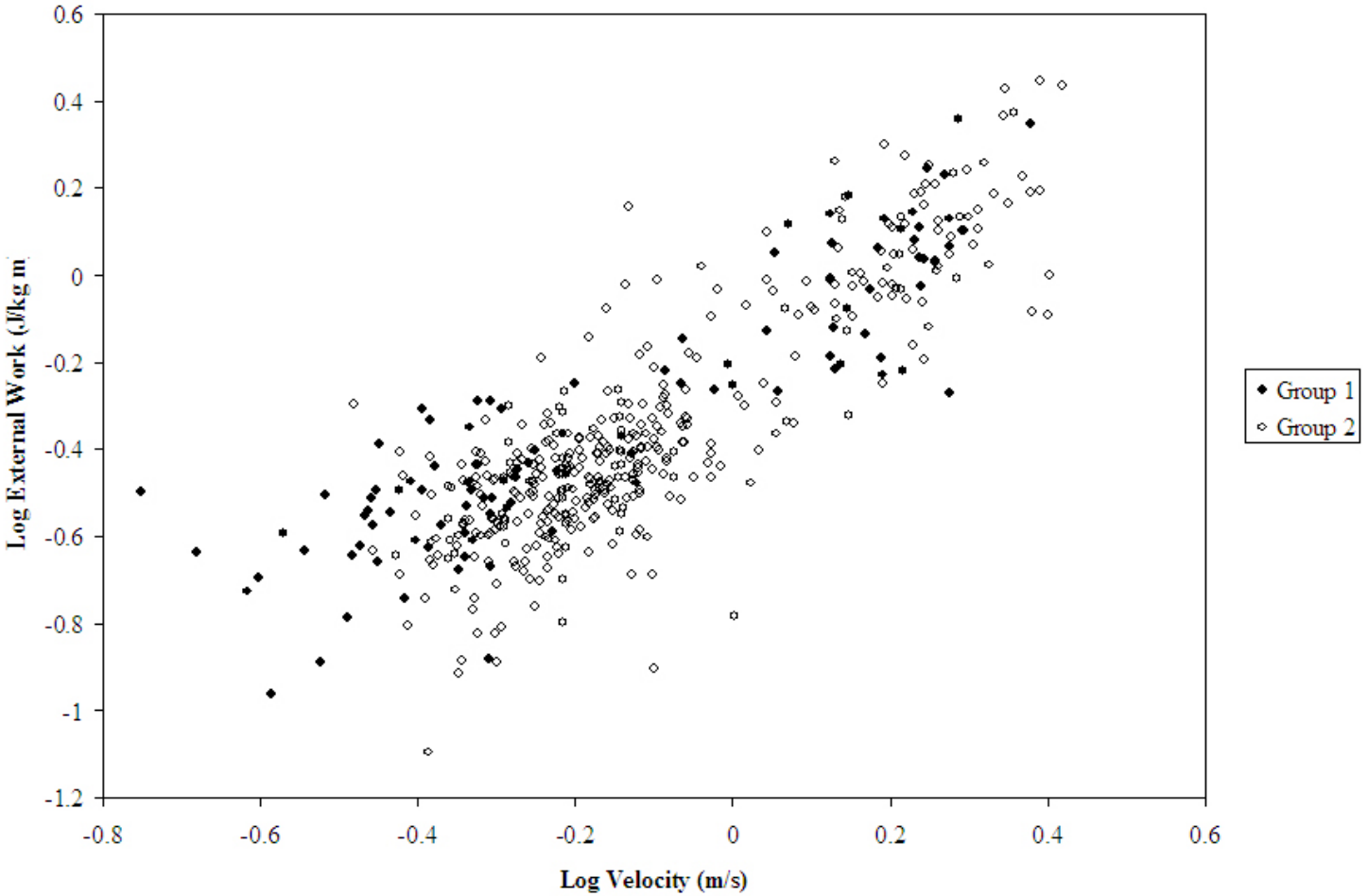


Figure 5.18. External work in the combined infant sample over the raw velocity range. External work is significantly higher in Group 1 compared to Group 2 of the combined sample.

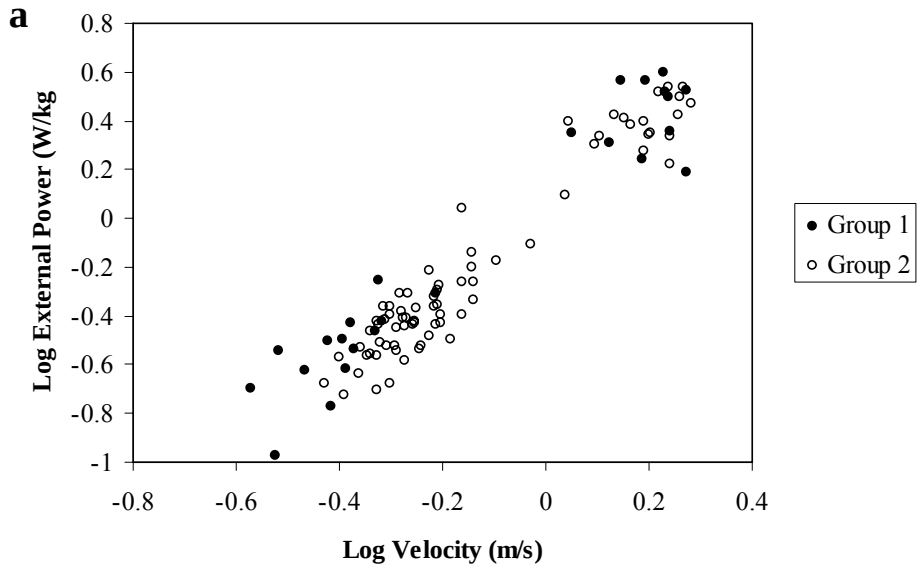


Figure 5.19a. External power in Infant 1 over the raw velocity range.

External power is significantly higher in Group 1 of Infant 1 compared to Group 2.

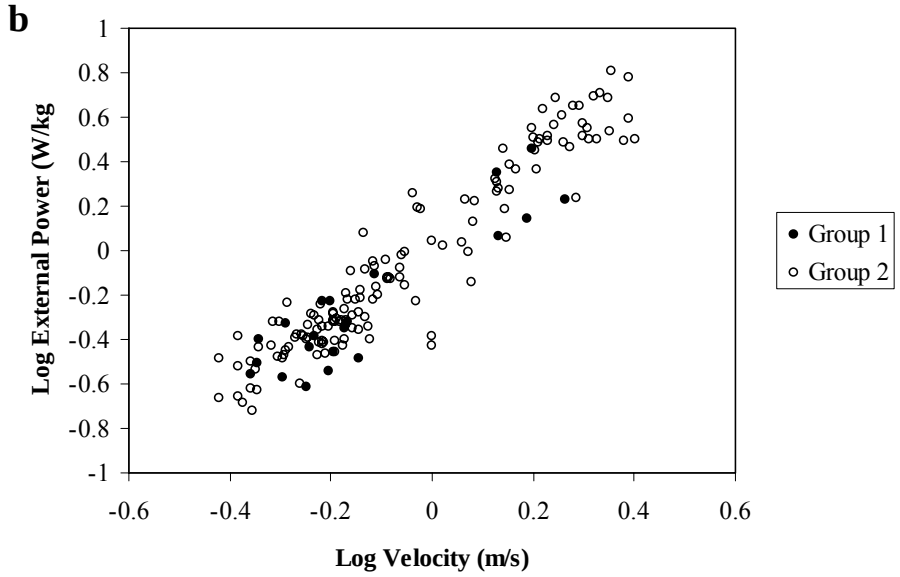


Figure 5.19b. External power in Infant 2 over the raw velocity range.

External power does not show significant between group differences for Infant 2.

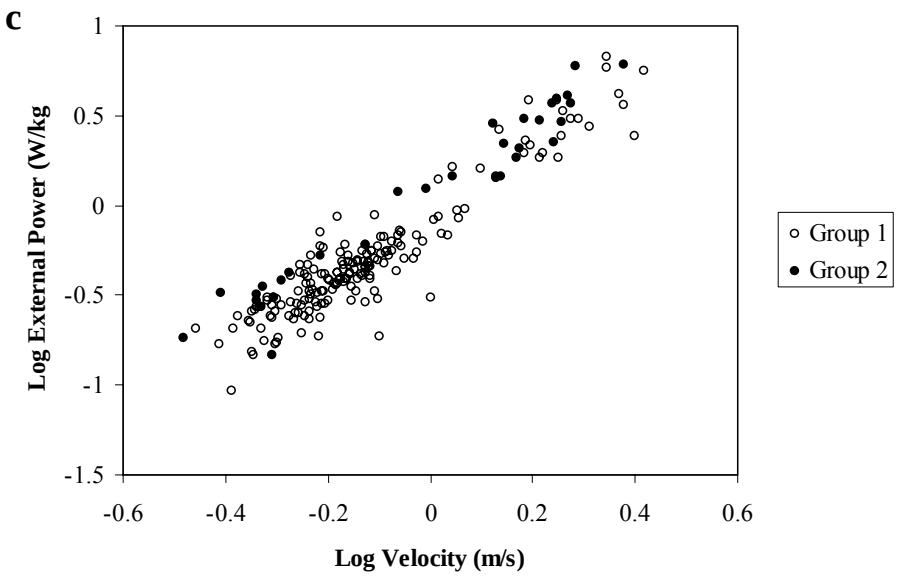


Figure 5.19c. External power in Infant 3 over the raw velocity range.

External power is significantly higher in Group 1 of Infant 3 compared to Group 2.

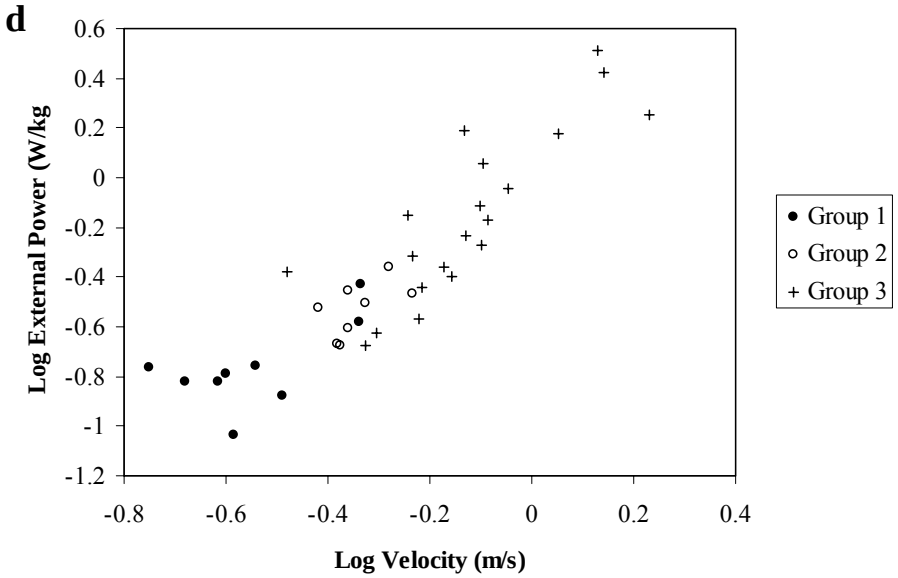


Figure 5.19d. External power in Infant 4 over the raw velocity range.

External power does not show significant between group differences for Infant 4.

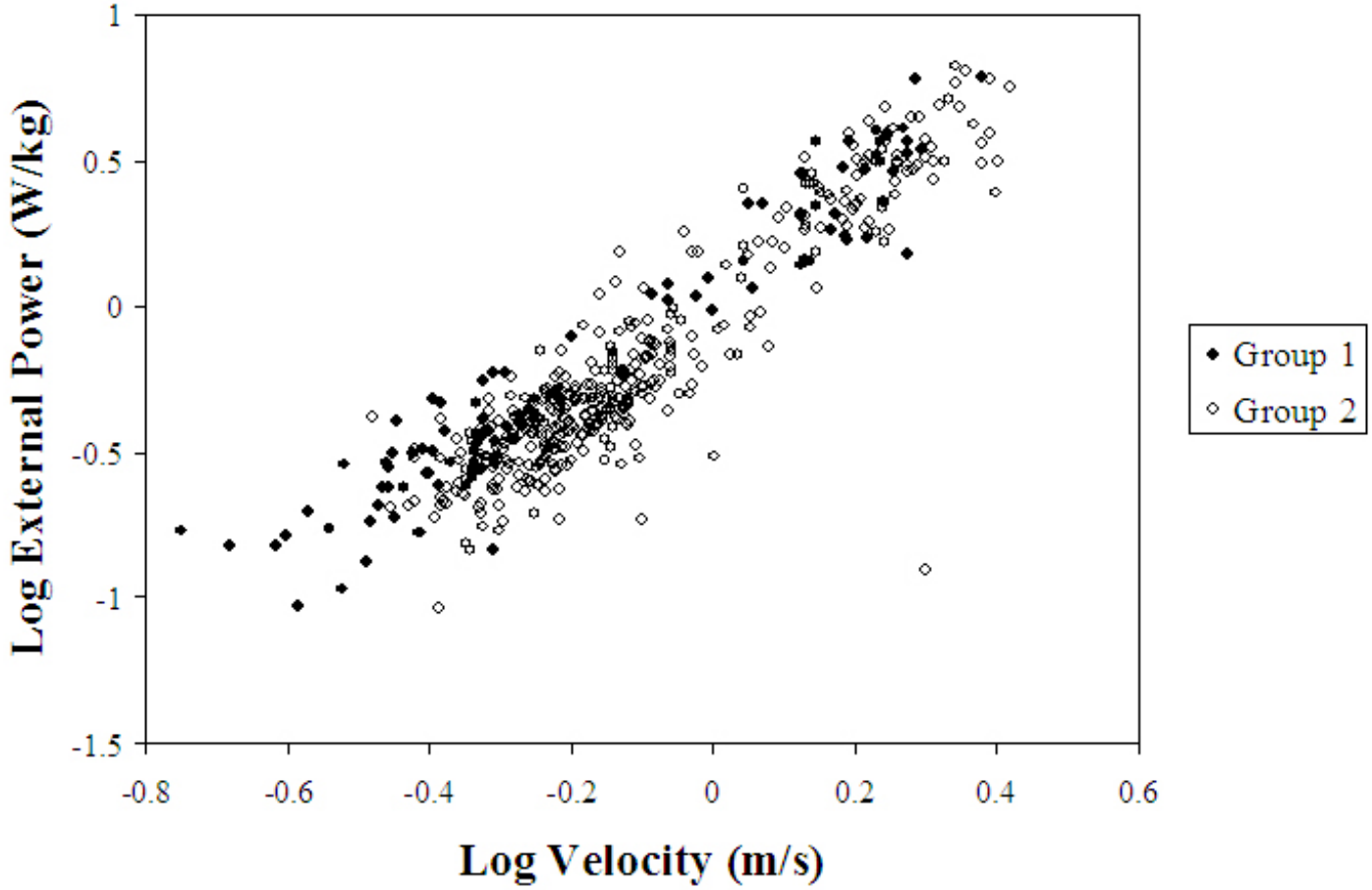


Figure 5.20. External power in the combined sample of infant baboons. External power is significantly higher in Group 1 of the combined sample.

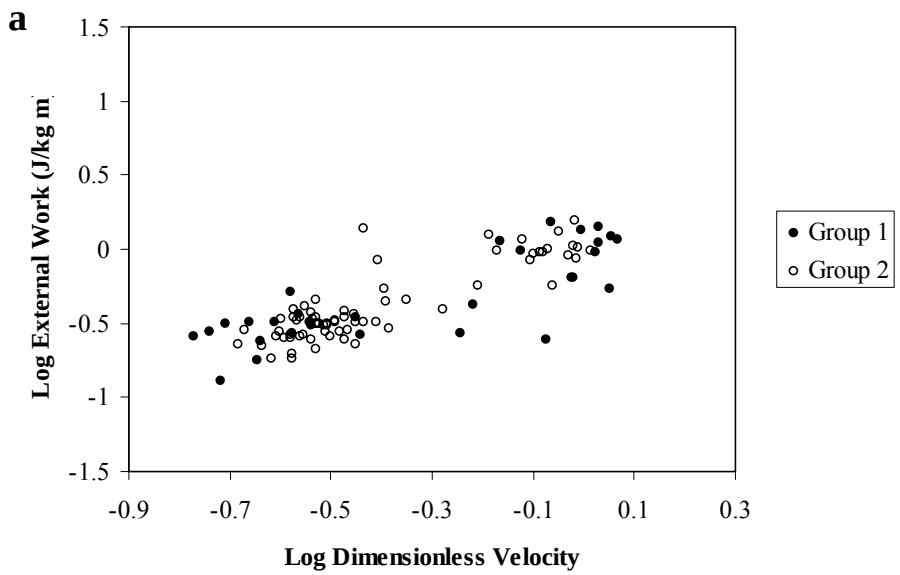


Figure 5.21a. External work in Infant 1 over the dimensionless velocity range. External work does not show significant between group differences in Infant 1.

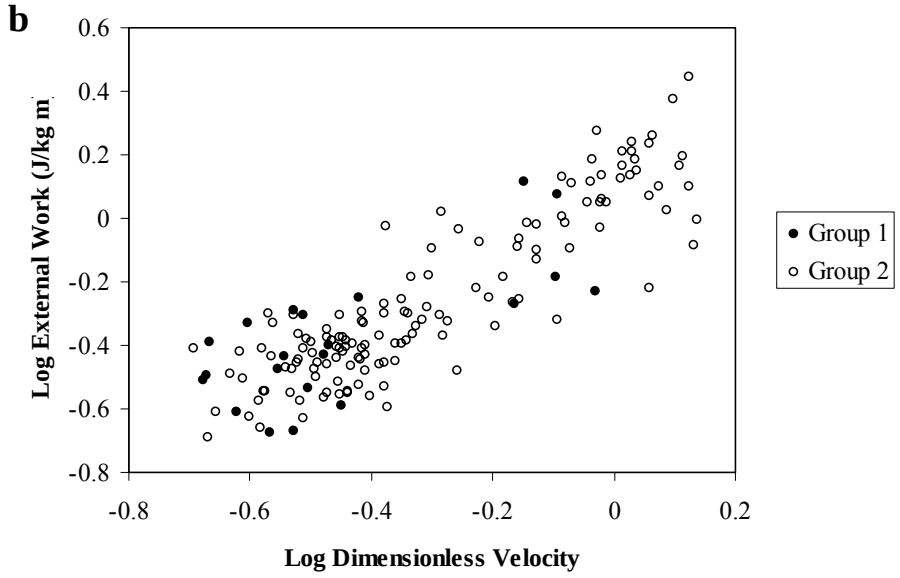


Figure 5.21b. External work in Infant 2 over the dimensionless velocity range. External work does not show significant between group differences in Infant 2.

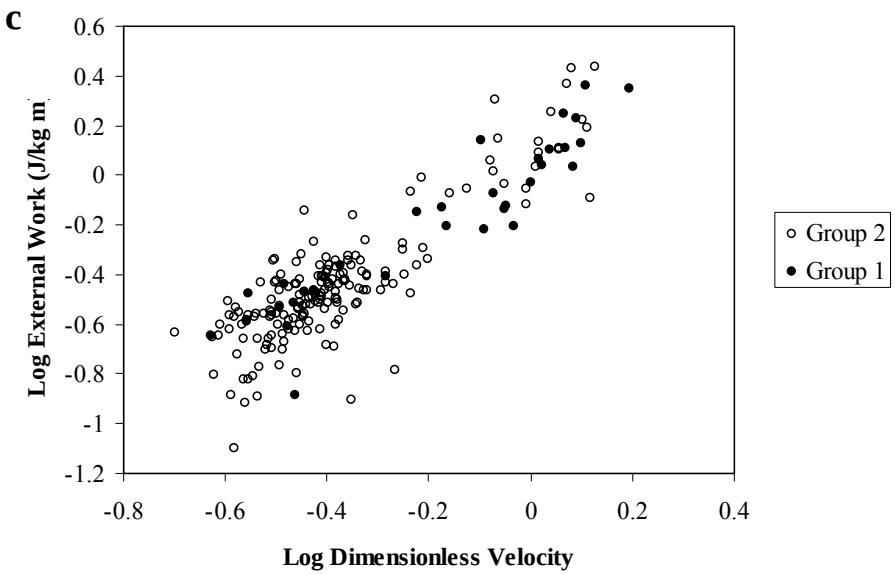


Figure 5.21c. External work in Infant 3 over the dimensionless velocity range. External work does not show significant between group differences in Infant 3.

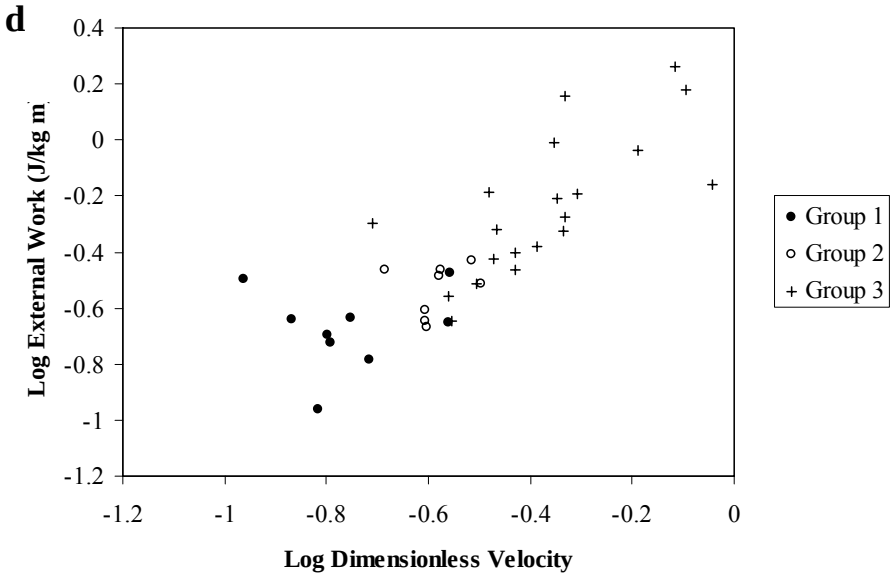


Figure 5.21d. External work in Infant 4 over the dimensionless velocity range. External work does not show significant between group differences in Infant 4.

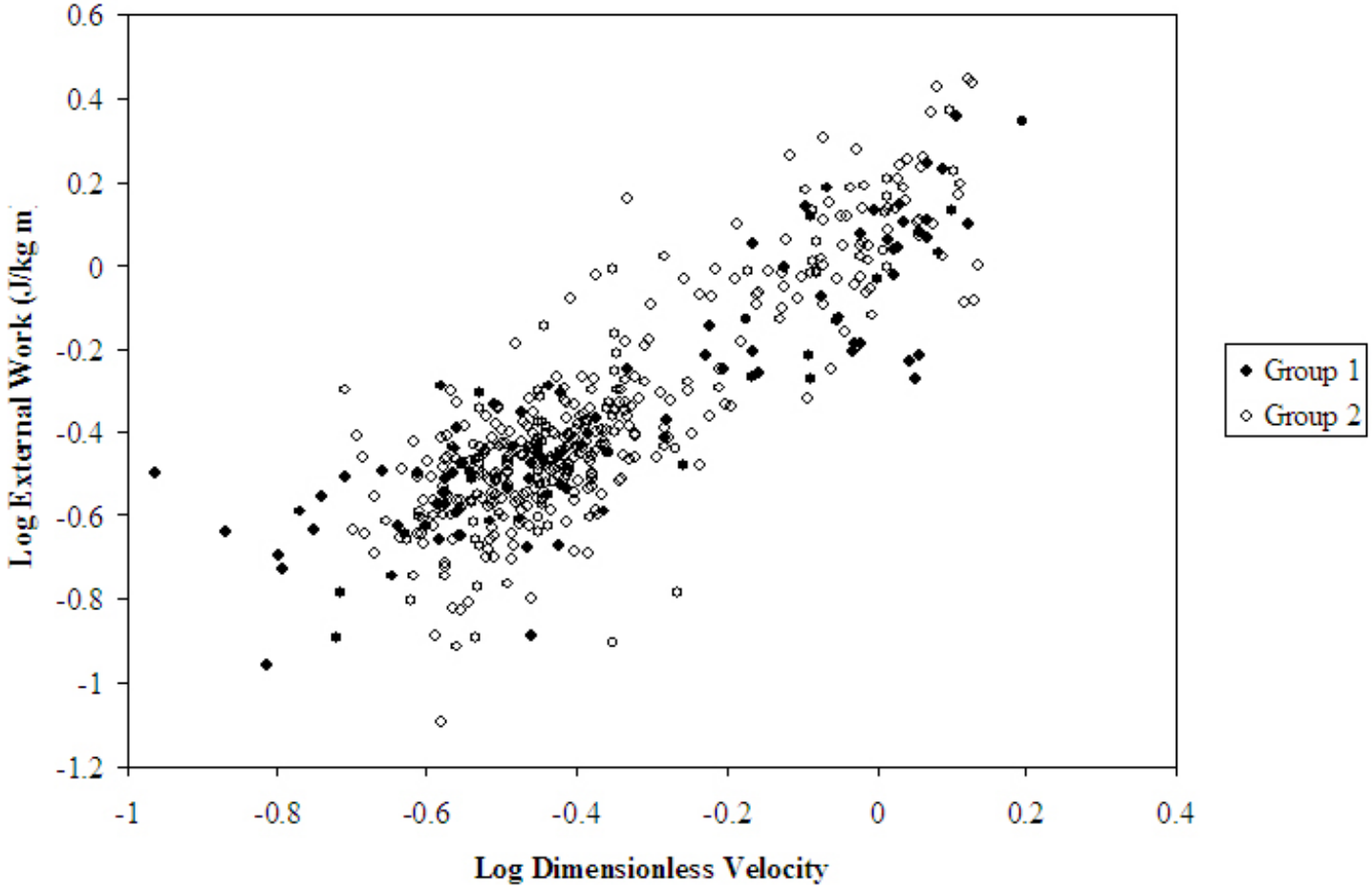


Figure 5.22. External work in combined infant sample over the dimensionless velocity range. External work shows no significant between group differences over the dimensionless velocity range in the combined sample of infant baboons.

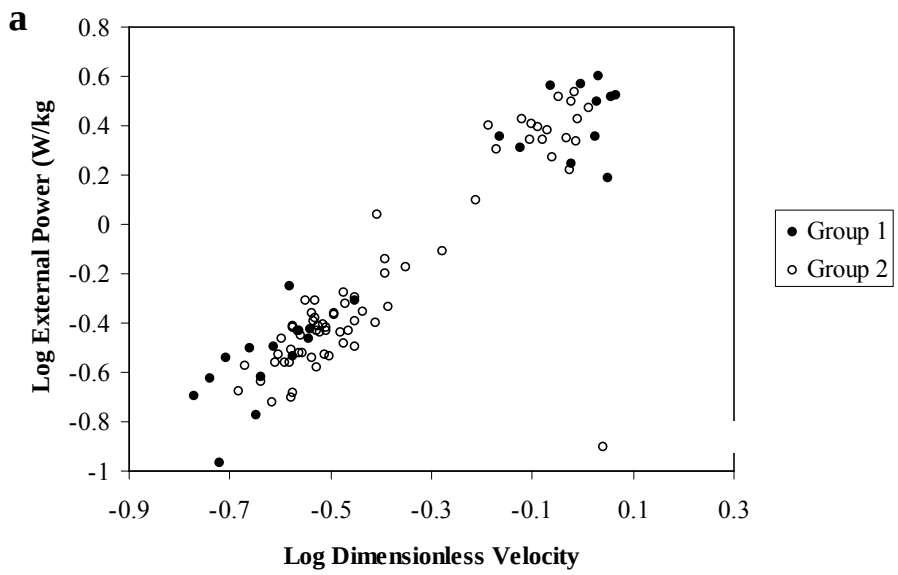


Figure 5.23a. External power in Infant 1 over the dimensionless velocity range. External power does not show significant between group differences in Infant 1.

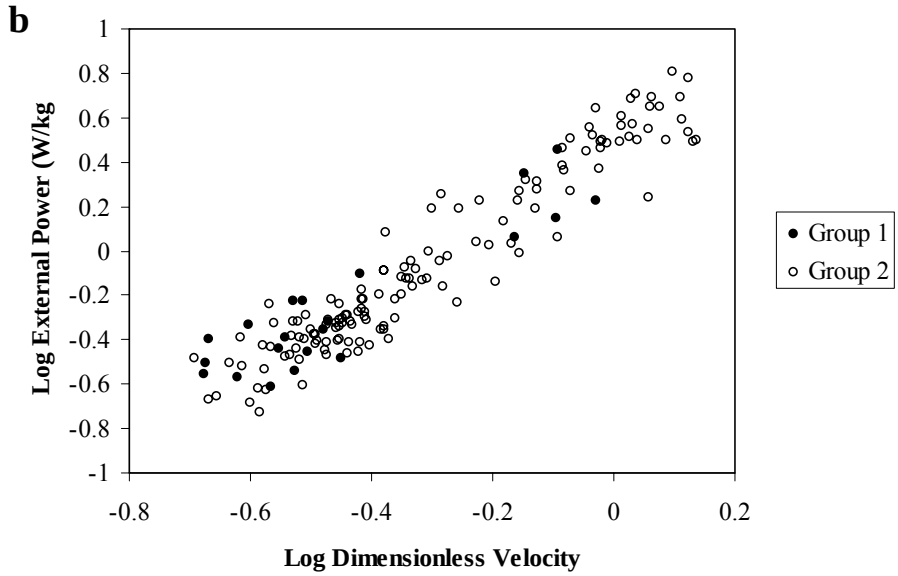


Figure 5.23b. External power in Infant 2 over the dimensionless velocity range. External power does not show significant between group differences in Infant 2.

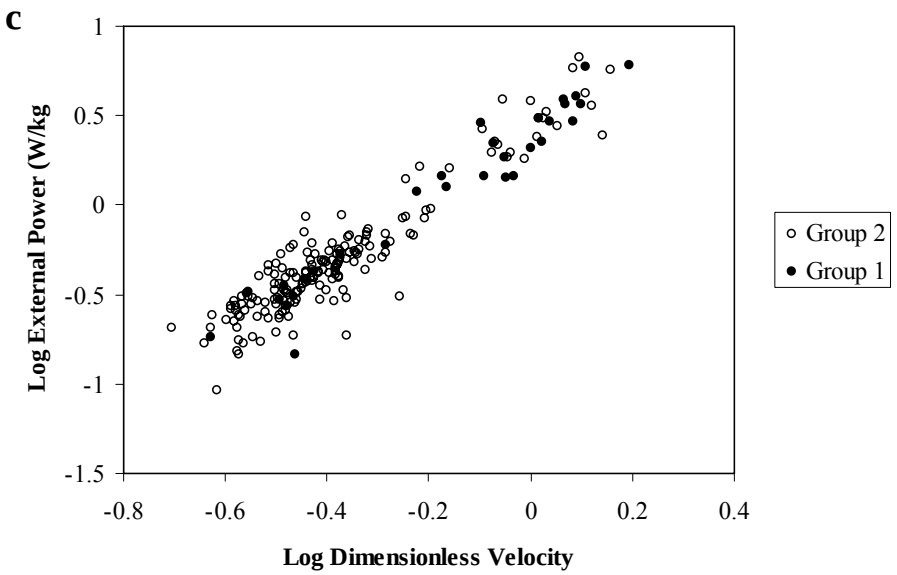


Figure 5.23c. External power in Infant 3 over the dimensionless velocity range. External power does not show significant between group differences in Infant 3.

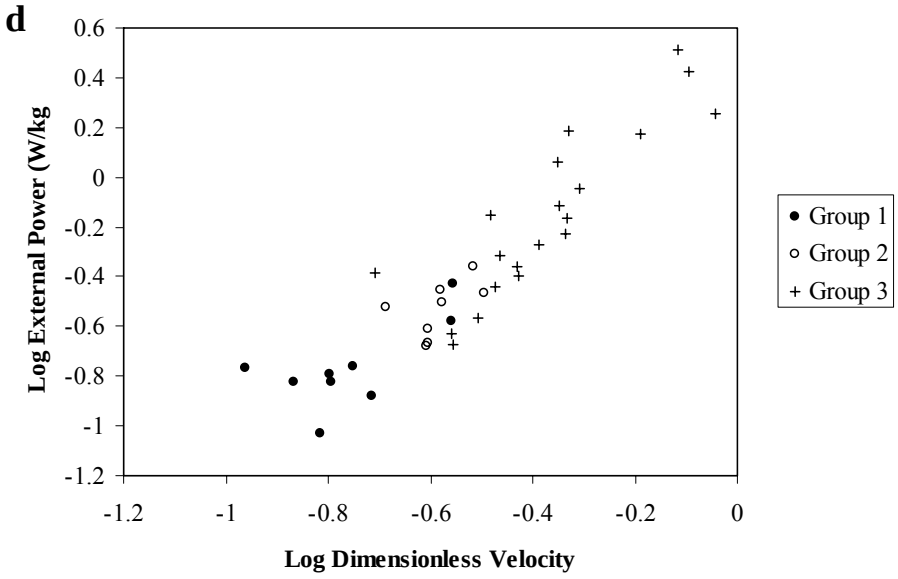


Figure 5.23d. External power in Infant 4 over the dimensionless velocity range. External power does not show significant between group differences in Infant 4.

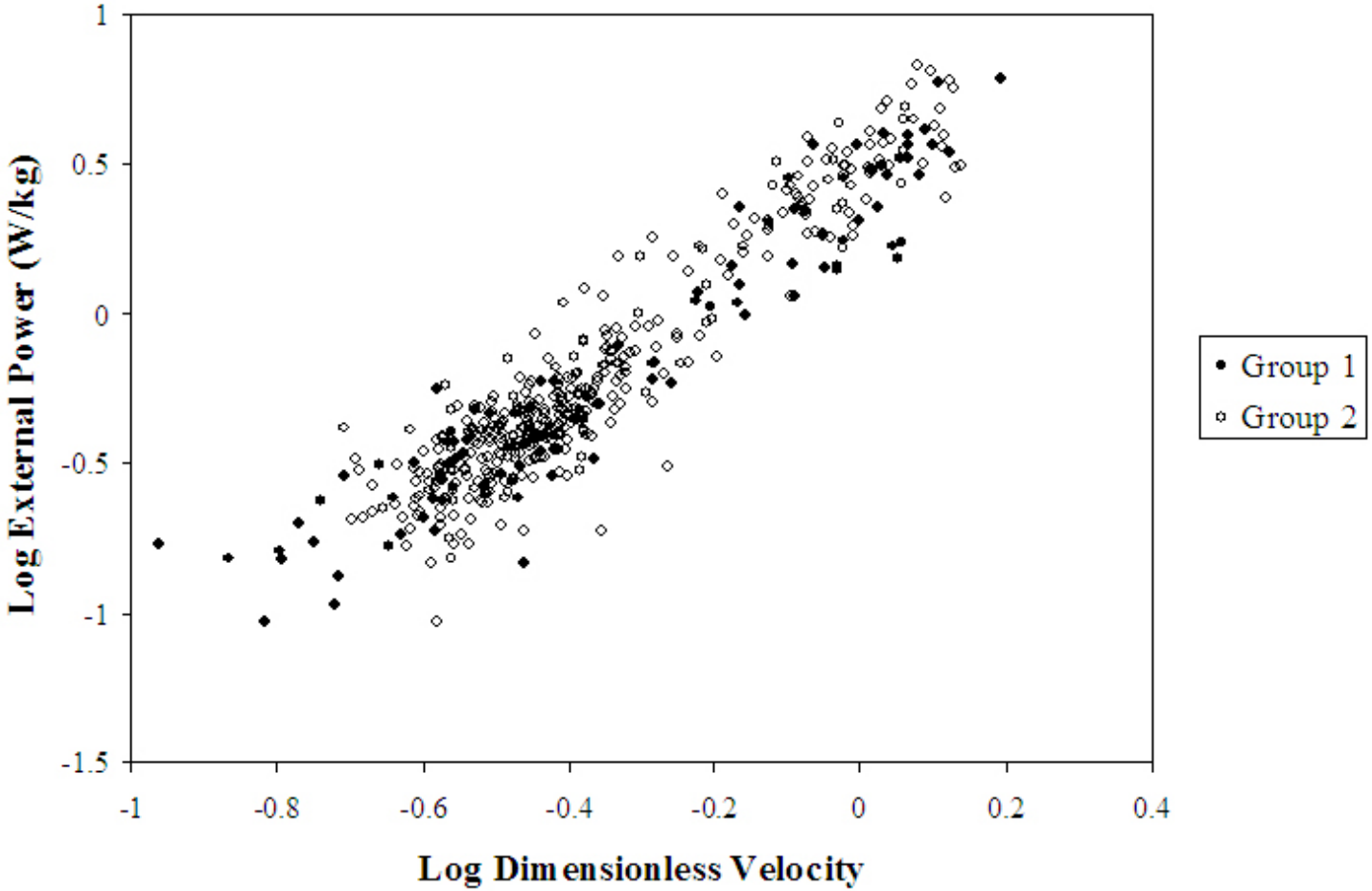


Figure 5.24. External power in the combined infant baboon sample of the dimensionless velocity range. External power shows no significant between group differences in the combined infant sample over the dimensionless velocity range.

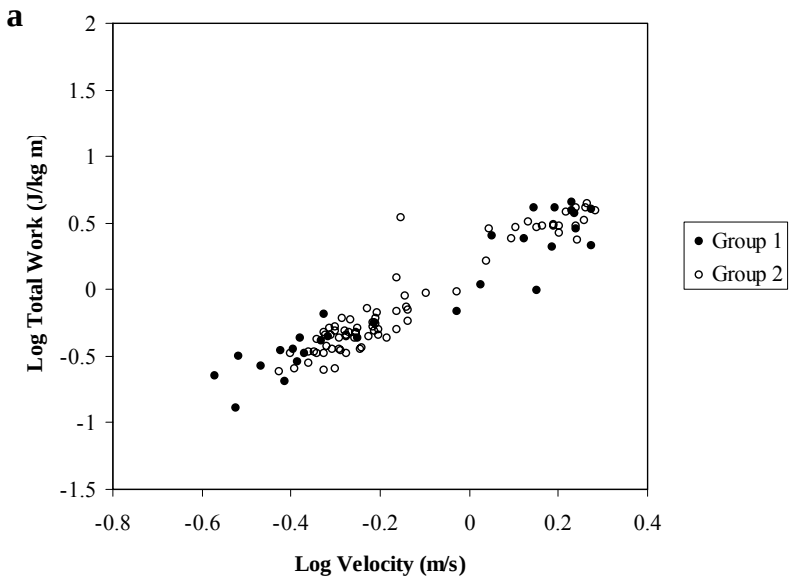


Figure 5.25a. Total work in Infant 1 over the raw velocity range.

Total work does not show between group differences in Infant 1.

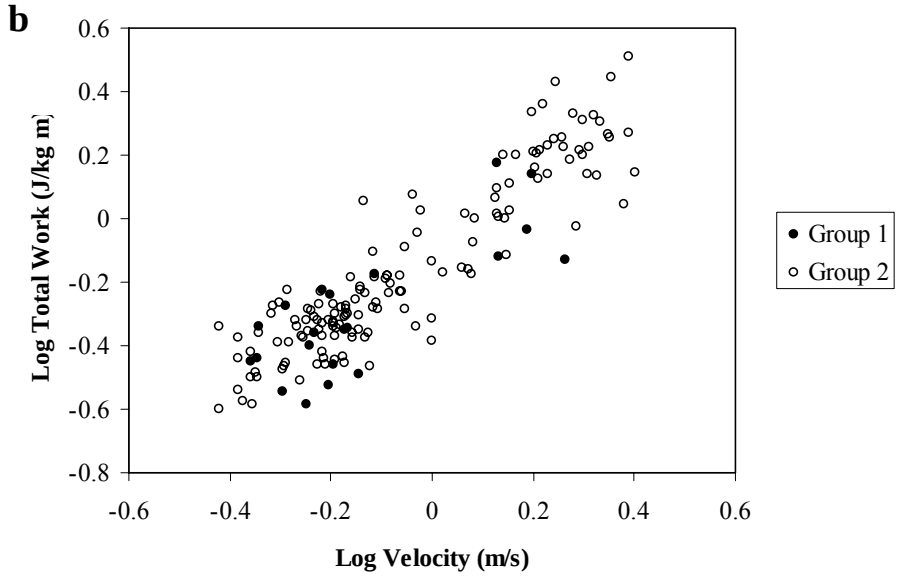


Figure 5.25b. Total work in Infant 2 over the raw velocity range.

Total work does not show between group differences in Infant 2.

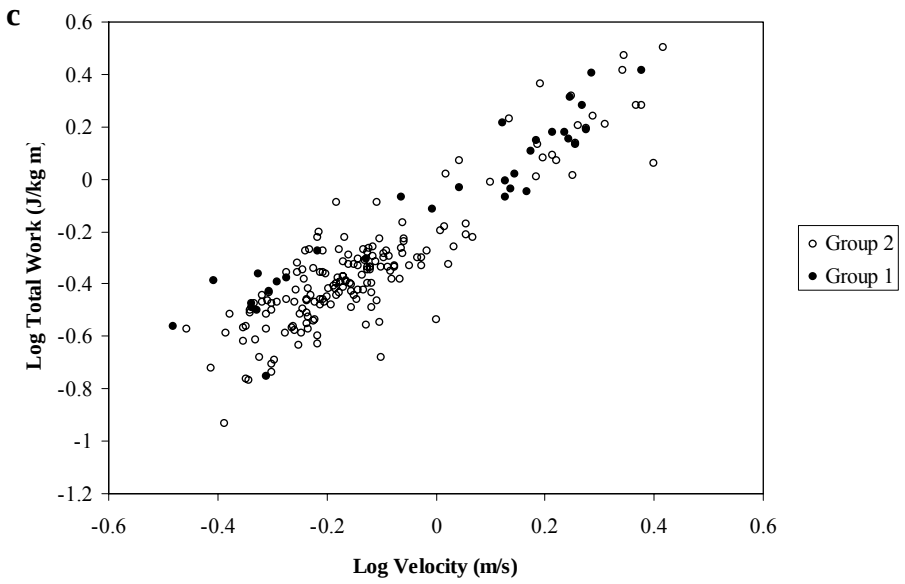


Figure 5.25c. Total work in Infant 3 over the raw velocity range.

Total work is significantly higher in Group 1 of Infant 3 at slower speeds.

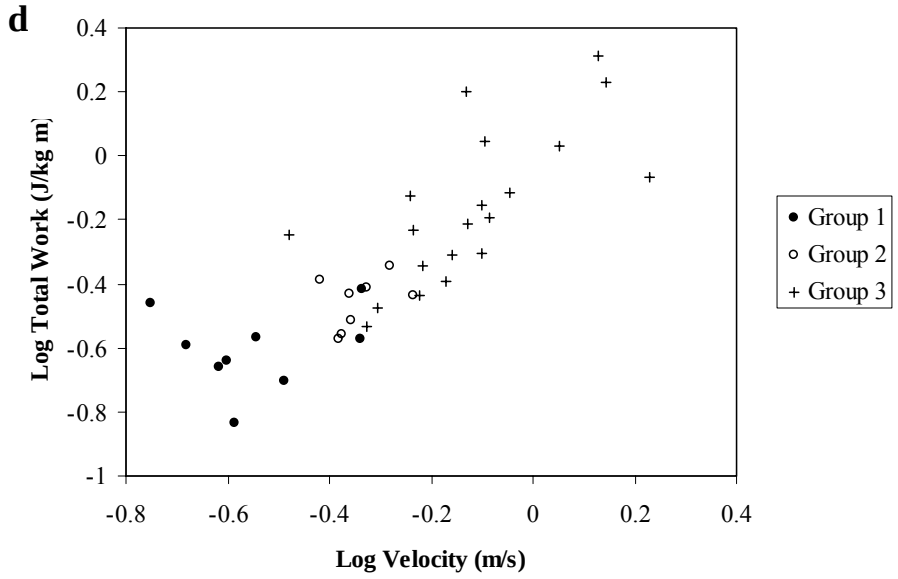


Figure 5.25d. Total work in Infant 4 over the raw velocity range.

Total work does not show between group differences in Infant 4.

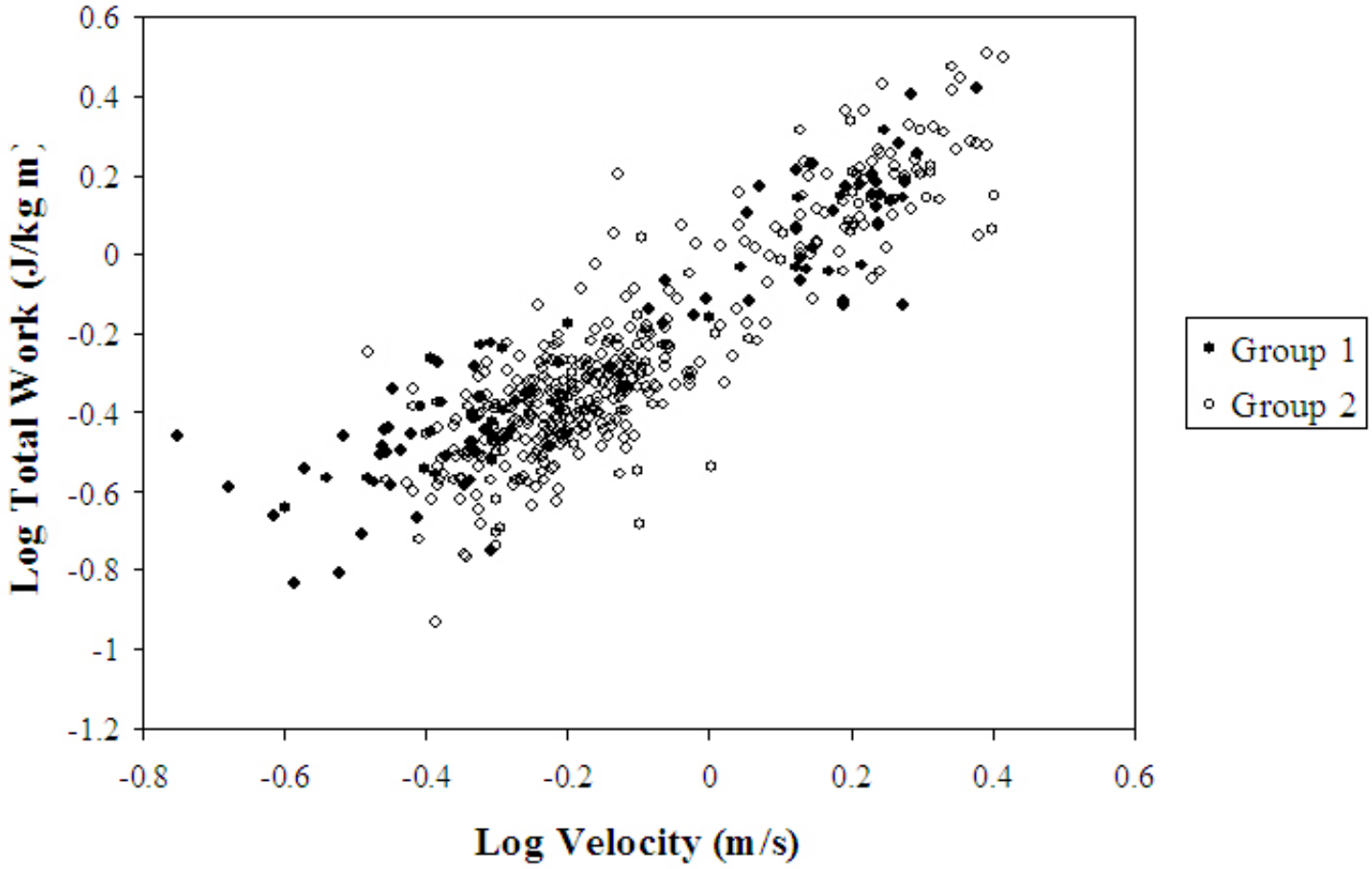


Figure 5.26. Total work in the combined sample of infant baboons over the raw velocity range. Total work is significantly higher in Group 1 individuals compared to Group 2 in the combined sample.

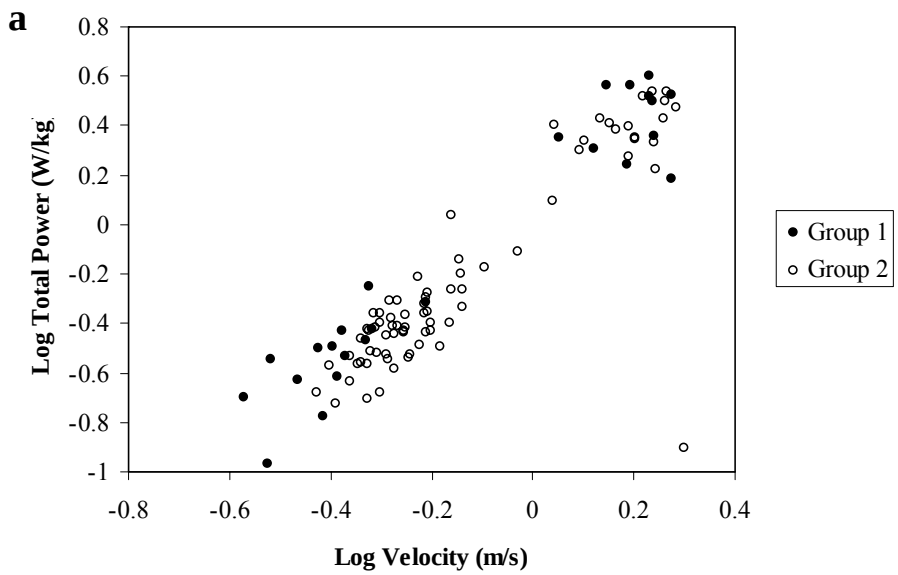


Figure 5.27a. Total power in Infant 1 over the raw velocity range.

Total power does not show significant between group differences in Infant 1.

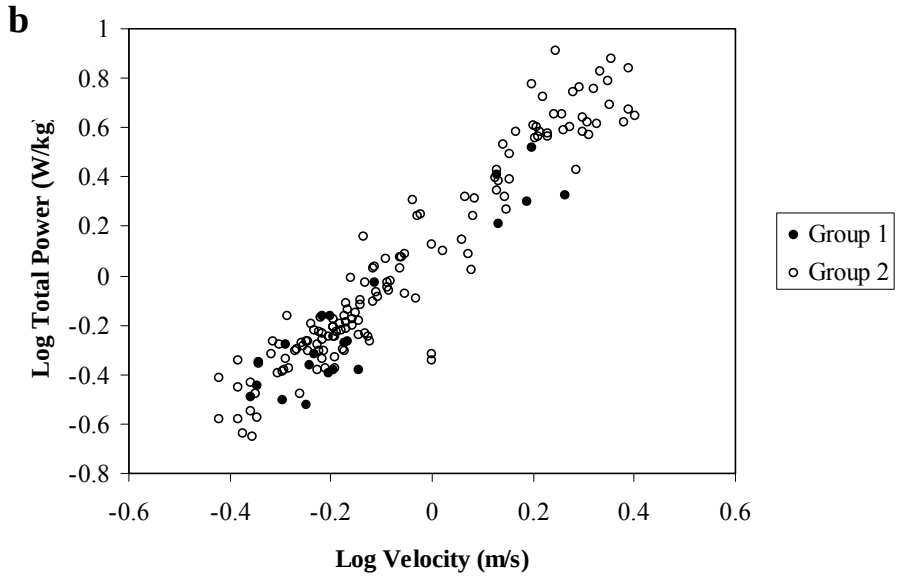


Figure 5.27b. Total power in Infant 2 over the raw velocity range.

Total power does not show significant between group differences in Infant 2.

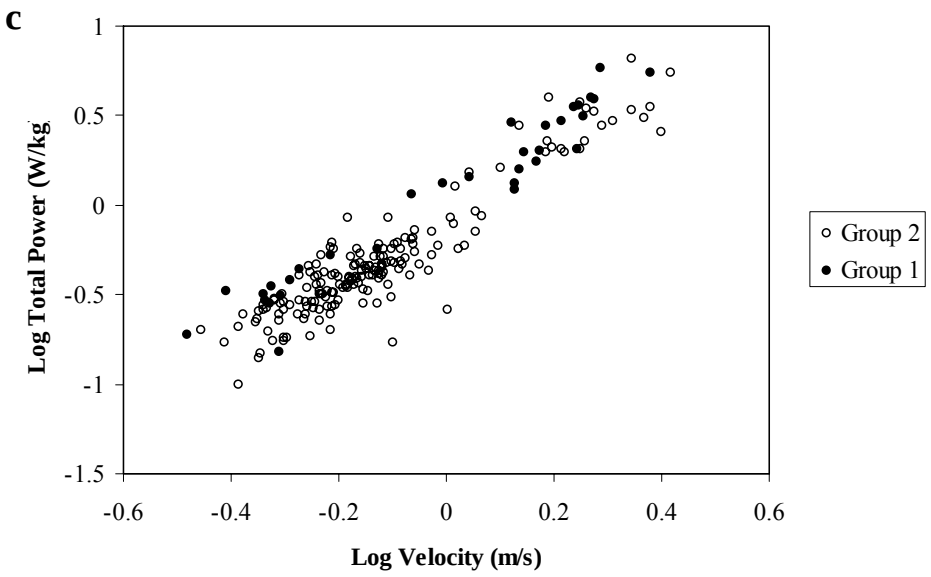


Figure 5.27c. Total power in Infant 3 over the raw velocity range.

Total power is significantly higher at slower speeds in Infant 3.

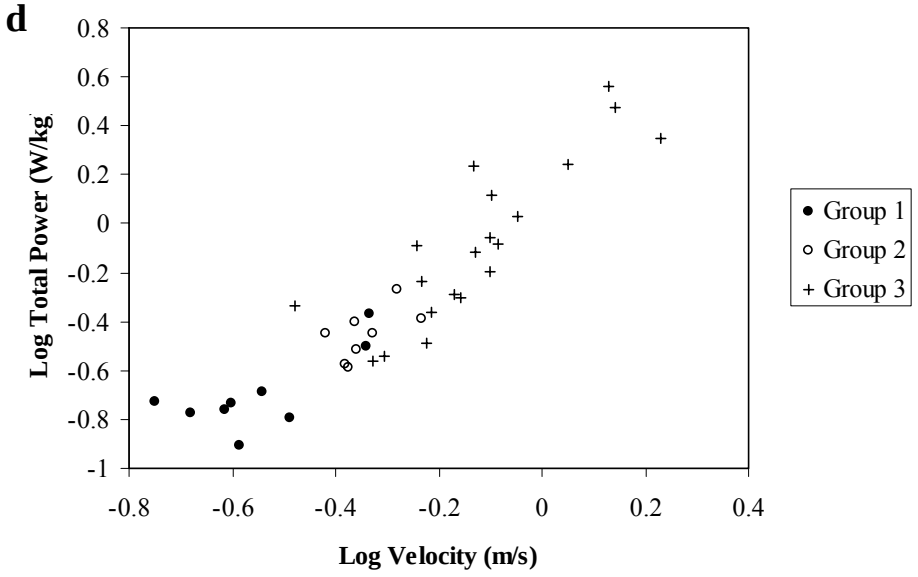


Figure 5.27d. Total power in Infant 4 over the raw velocity range.

Total power does not show significant between group differences in Infant 4.

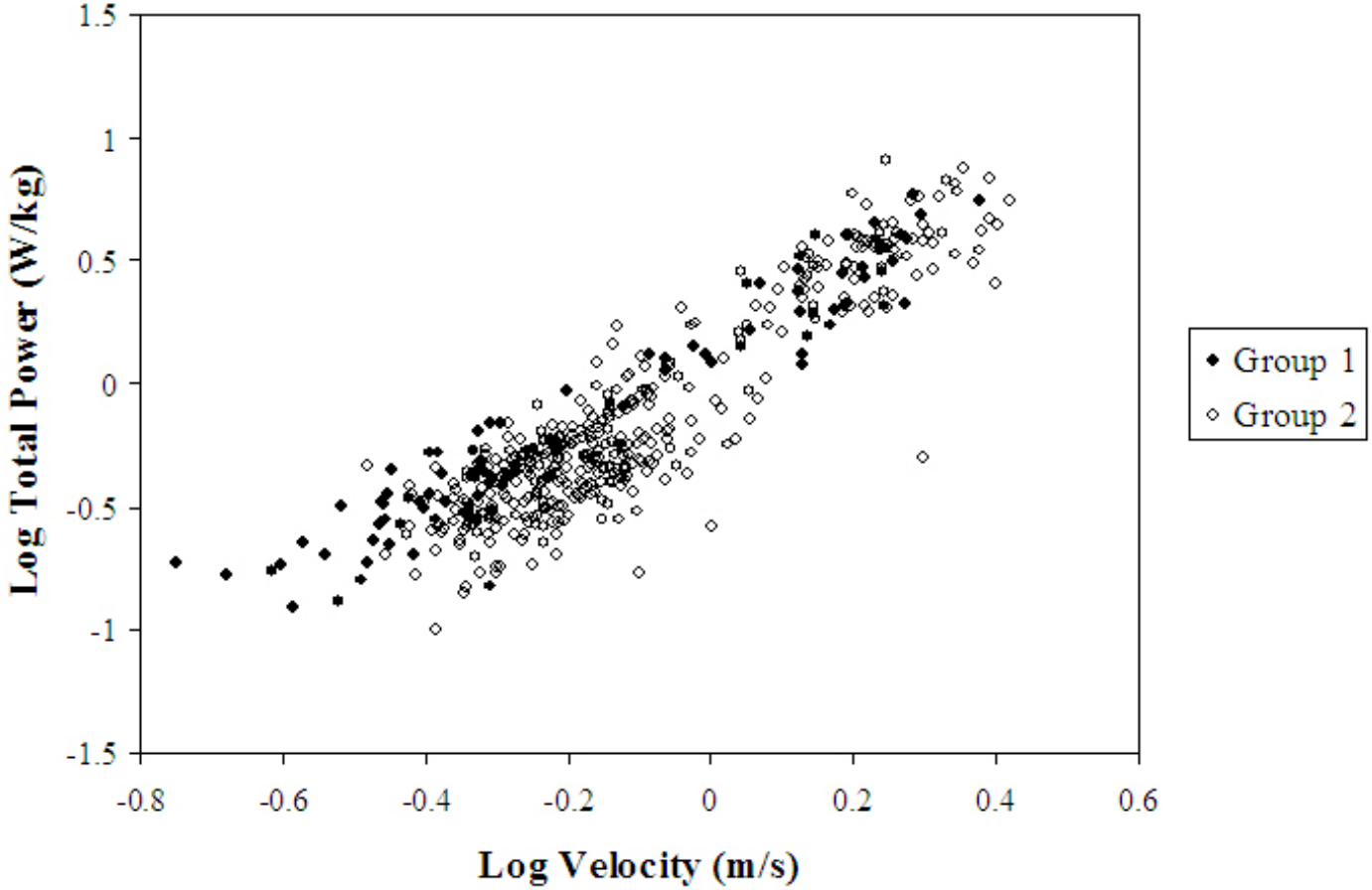


Figure 5.28. Total power in the combined infant baboon sample over the raw velocity range. Total power is significantly higher in Group 1 individuals compared to Group 2.

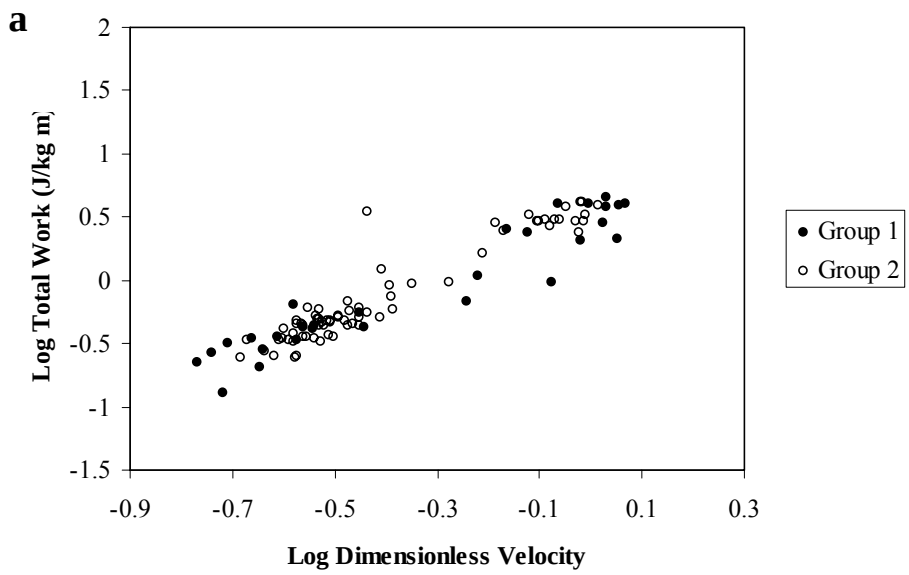


Figure 5.29a. Total work in Infant 1 over the dimensionless velocity range. Total work does not show significant between group differences in Infant 1.

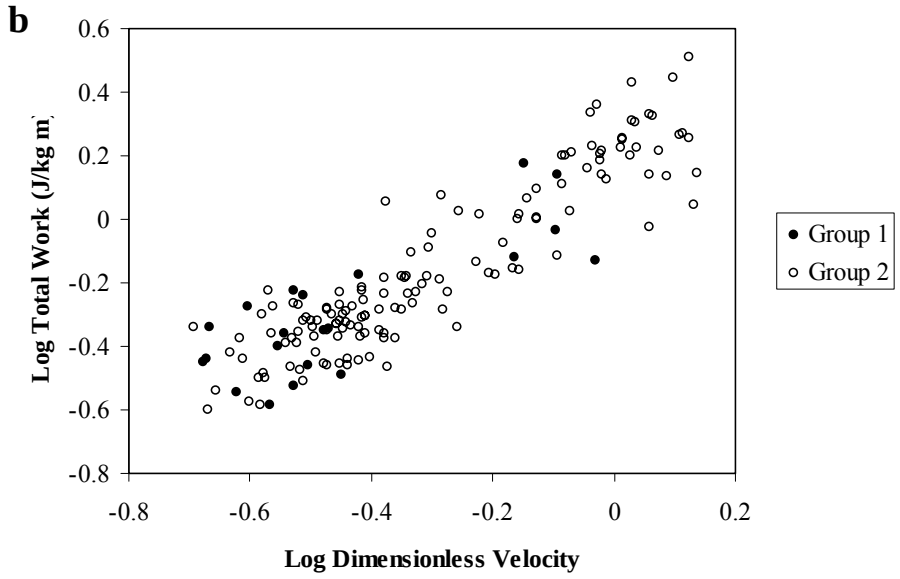


Figure 5.29b. Total work in Infant 2 over the dimensionless velocity range. Total work does not show significant between group differences in Infant 2.

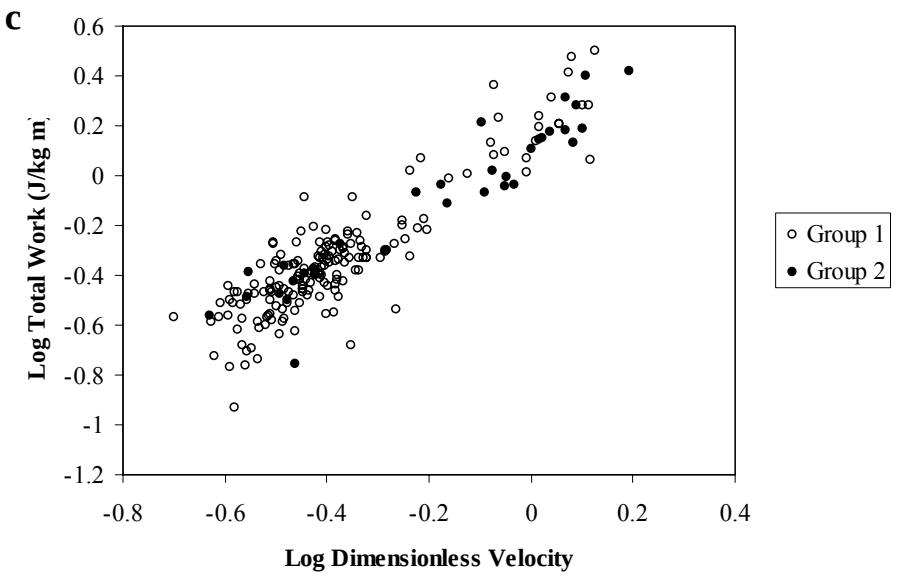


Figure 5.29c. Total work in Infant 3 over the dimensionless velocity range.

Total work is significantly higher in Group 1 compared to Group 2, but this difference mostly occurs at low speeds.

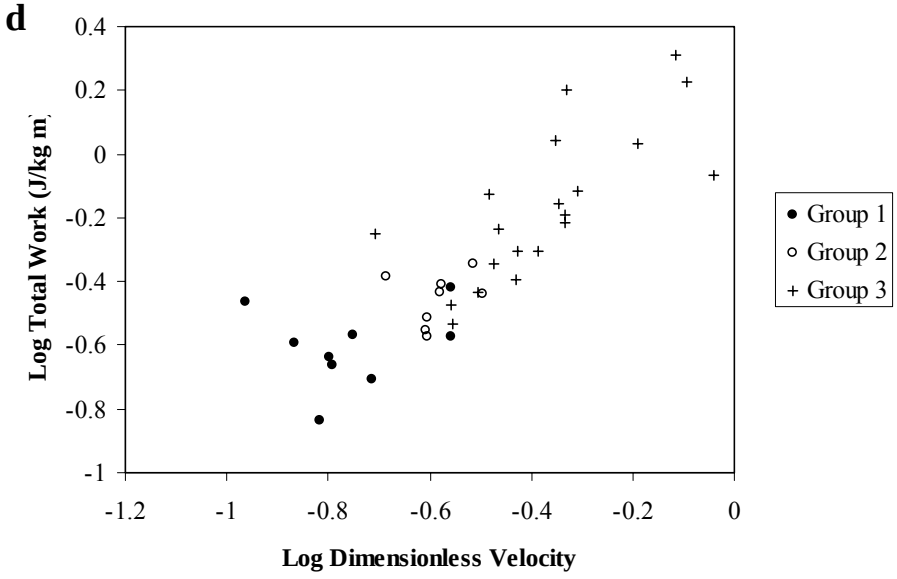


Figure 5.29d. Total work in Infant 4 over the dimensionless velocity range.

Total work does not show significant between group differences in Infant 4.

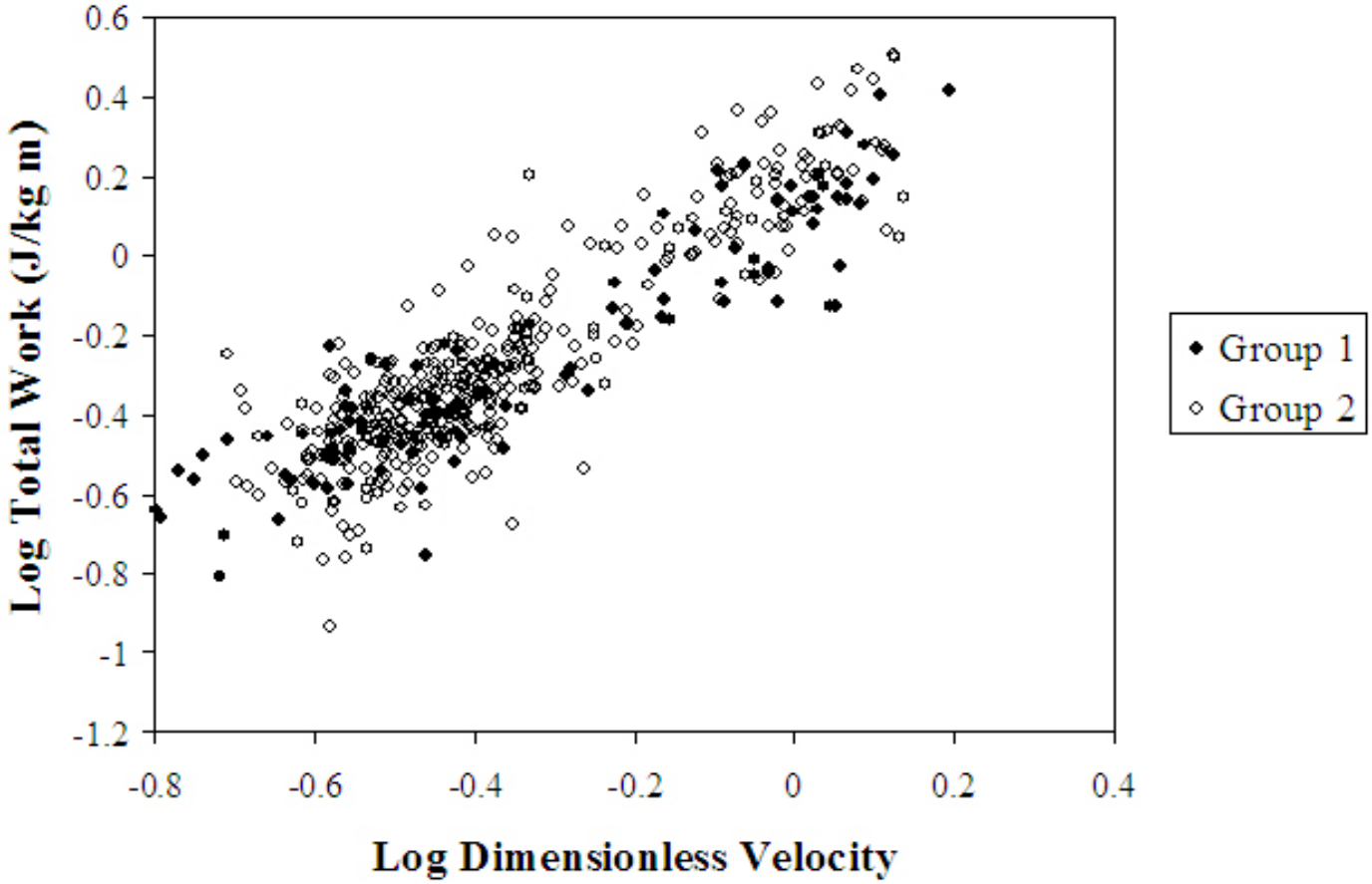


Figure 5.30. Total work in the combined infant baboon sample over the raw velocity range. Total work does not show significant between group differences over the dimensionless velocity range.

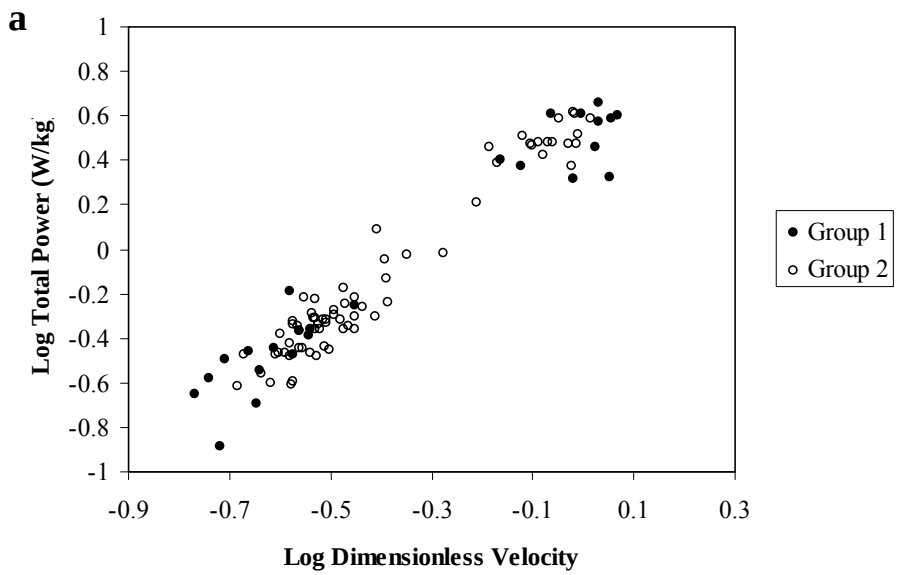


Figure 5.31a. Total power in Infant 1 over the raw velocity range.

Total power shows no significant between group differences in Infant 1.

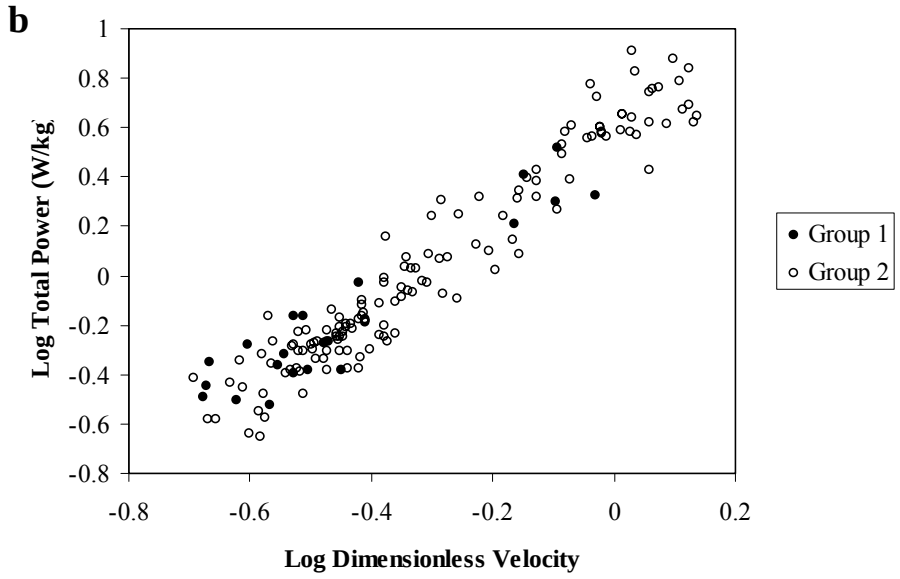


Figure 5.31b. Total power in Infant 2 over the raw velocity range.

Total power shows no significant between group differences in Infant 2.

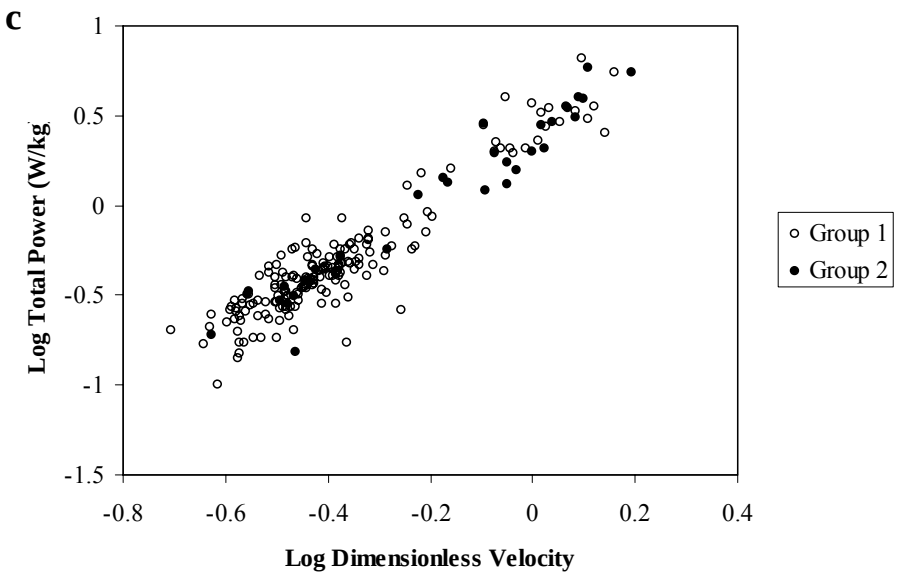


Figure 5.31c. Total power in Infant 3 over the raw velocity range.

Total power shows no significant between group differences in Infant 3.

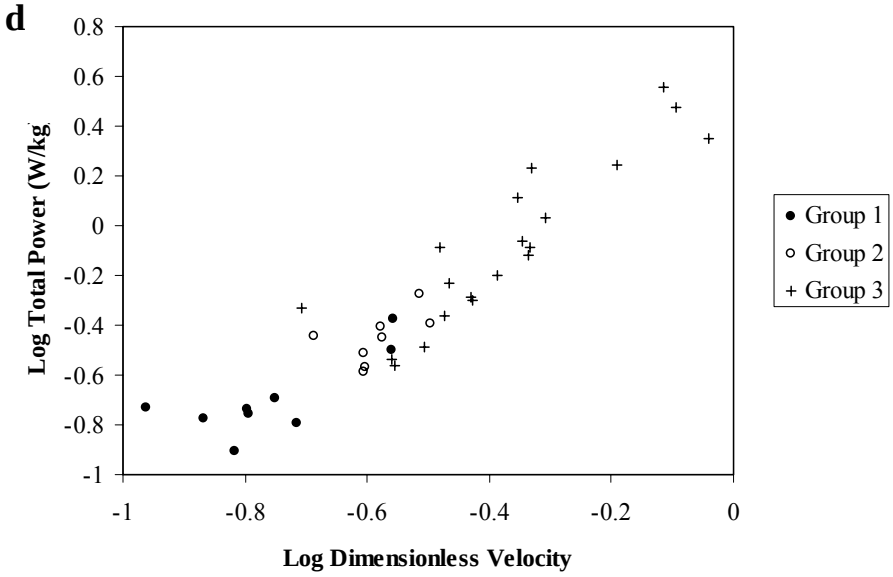


Figure 5.31d. Total power in Infant 4 over the raw velocity range.

Total power shows no significant between group differences in Infant 4.

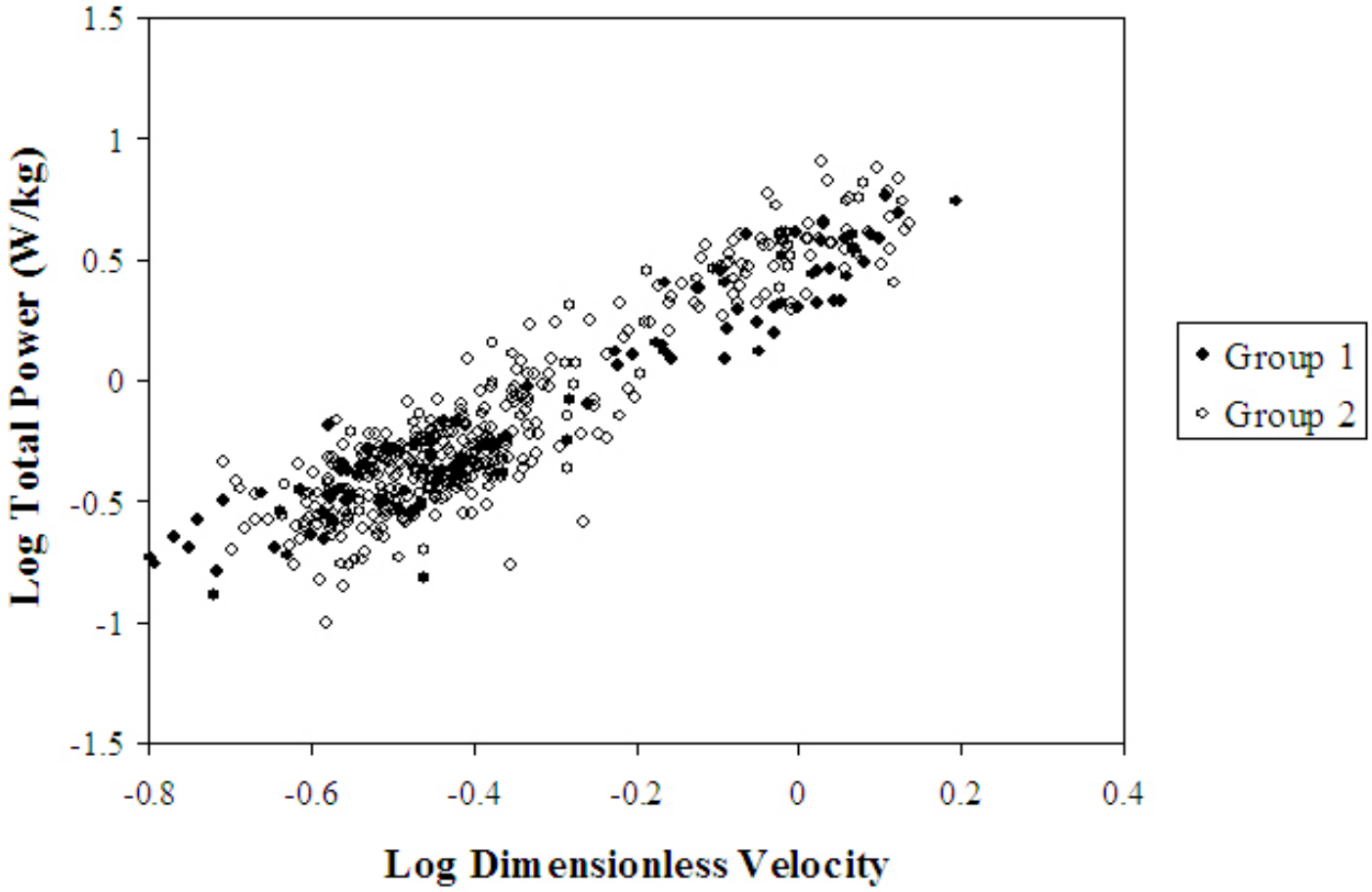


Figure 5.32. Total power in combined infant baboon sample over the dimensionless velocity range. Total power shows no significant between group differences in the combined infant baboon sample over the dimensionless velocity range.

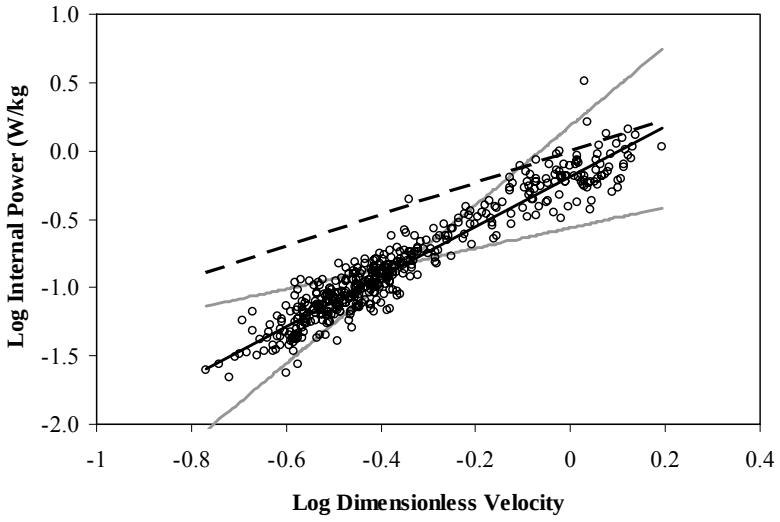


Figure 5.33. Comparison of internal power in infant baboons and dogs.

Internal power in infant baboons (open circles) and dogs (dashed line). Dog data from Fedak et al. (1982). Gray lines are the 95% confidence intervals of the infant baboon least-squares regression line (solid black line).

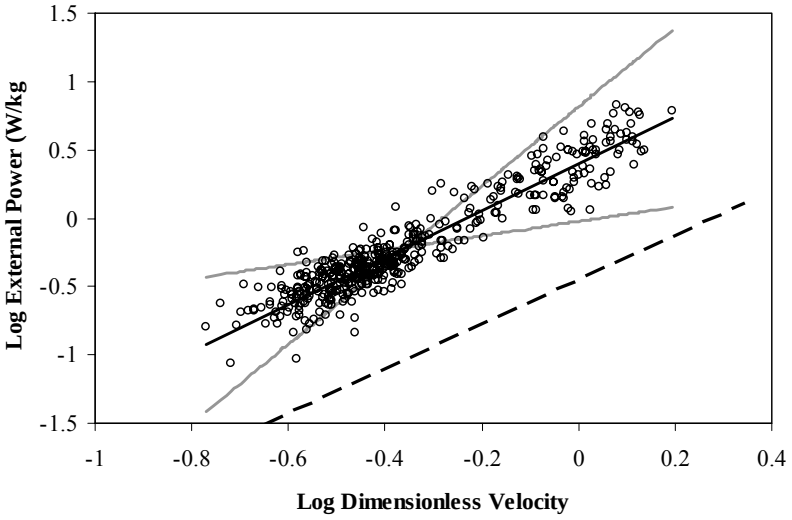


Figure 5.34. Comparison of external power in infant baboons and dogs.

External power in infant baboons (open circles) and dogs (dashed line). Dog data from Heglund et al. (1982). Gray lines are the 95% confidence intervals of the infant baboon least-squares regression line (solid black line).

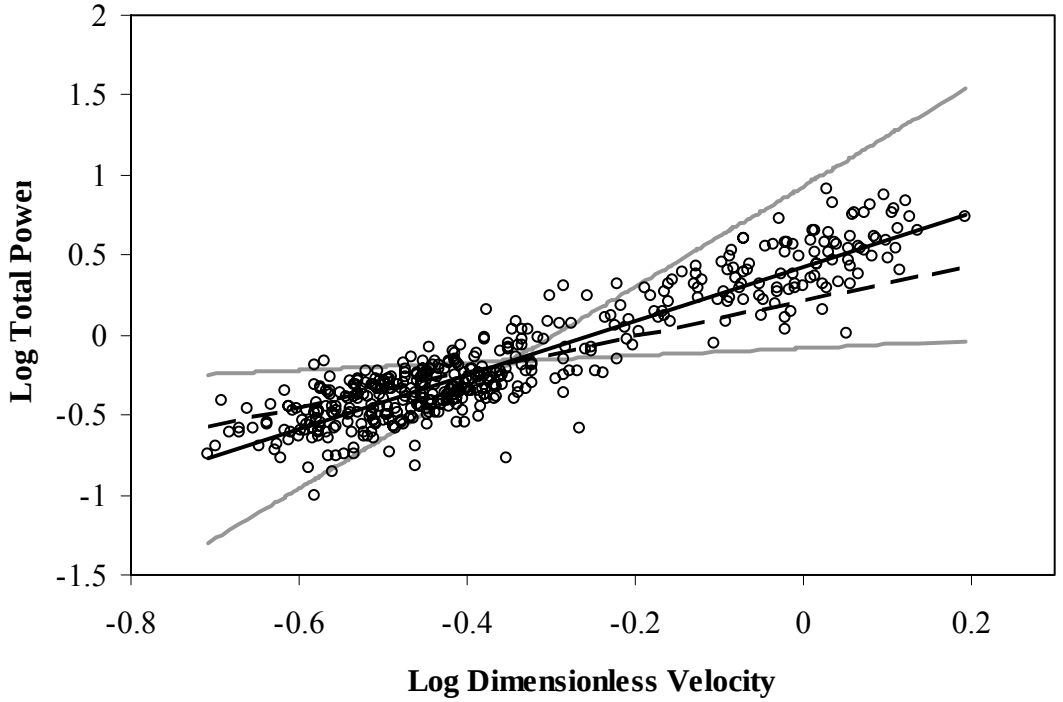


Figure 5.35. Comparison of total power in infant baboons and dogs.

Total power in infant baboons (open circles) and dogs (dashed line). Dog data from Heglund et al. (1982). Gray lines are the 95% confidence intervals of the infant baboon least-squares regression line (solid black line).

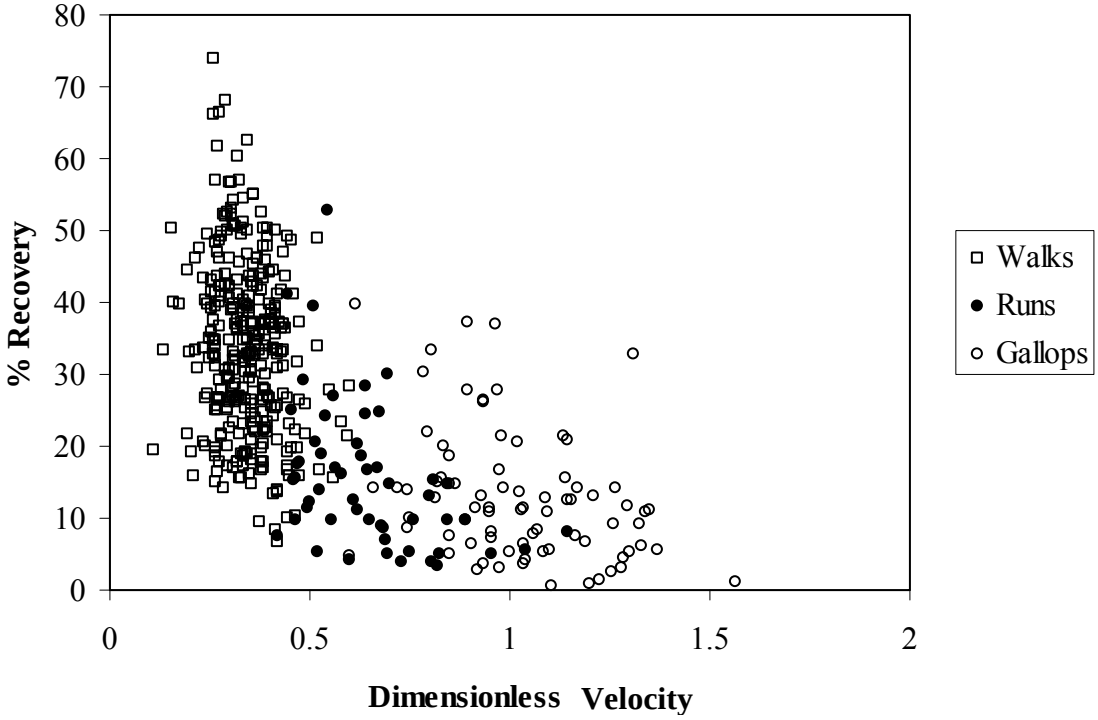


Figure 5.36. Percent recovery in the infant baboon sample as a function of dimensionless velocity.

The percentage of energy recovered by a pendular exchange of potential and kinetic energy decreases with increasing dimensionless velocity as the infant baboons transition from a walk (open squares) to a run (closed circles) and finally to a gallop (open circles).

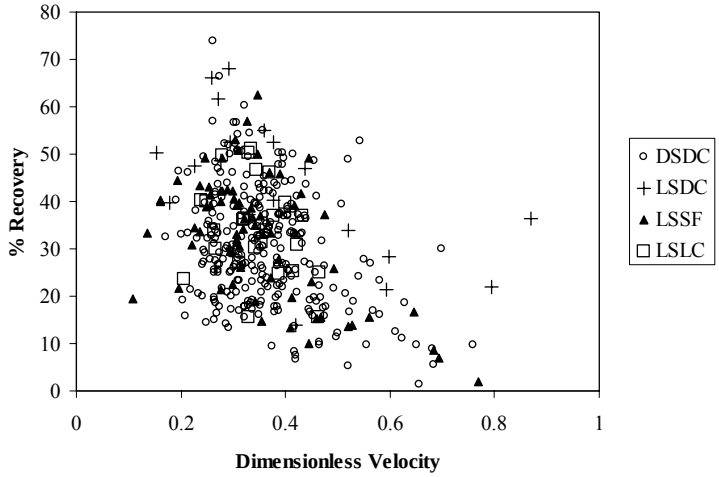


Figure 5.37. The effects of footfall sequence on percent recovery in the combined infant baboon sample at walking velocities. Footfall sequences have no effect on the percent of energy recovered by pendular mechanisms in the infant baboon sample. The following gaits are shown above: diagonal sequence diagonal couplet (DSDC; open circles), lateral sequence lateral couplet (LSDC; plus signs), lateral sequence single foot (LSSF; closed triangles), and lateral sequence lateral couplet (LSLC; open squares).

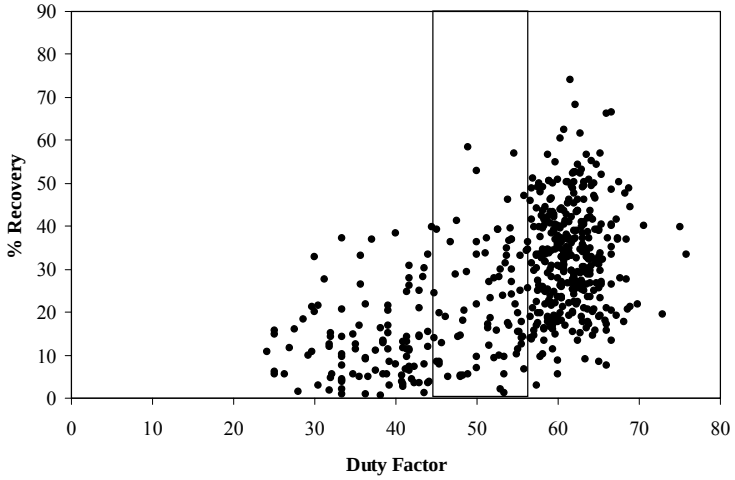


Figure 5.38. Percent recovery at the walk-run transition in infant baboons.

Percent recovery shown as a function of duty factor (the percentage of the stride a hindfoot is on the ground). Gray shaded area indicates the transition between fast walks and slow runs.

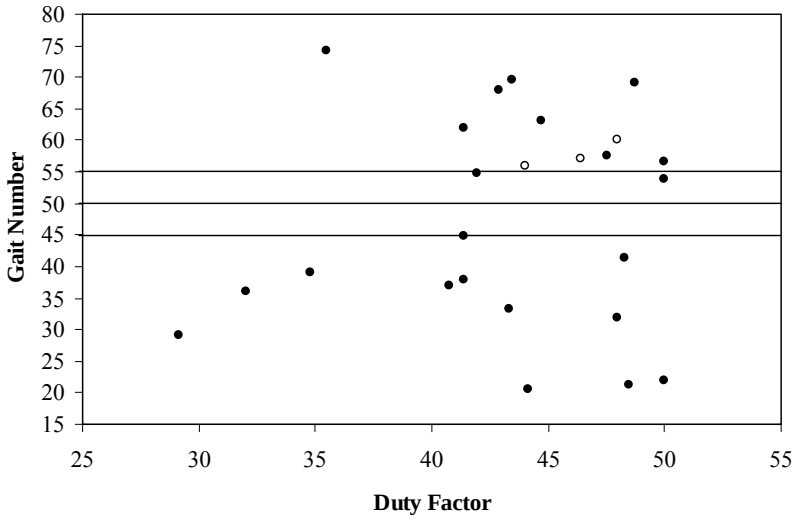


Figure 5.39. Footfall sequences during the running gaits of the infant baboons

Gait number is the percentage of the stride a forelimb touchdown follows the ipsilateral hindlimb touchdown. A gait number of 50 indicates a trot, where the forelimb touches down at the same time as the contralateral hindlimb. Gait numbers above 50 indicate the forelimb touches down after the contralateral hindlimb and gait numbers below 50 indicate the forelimb touches down before the contralateral hindlimb. Closed circles are ambles, open circles are runs with an aerial phase. The solid black lines show the range of gait numbers normally considered a trot in quadrupeds.

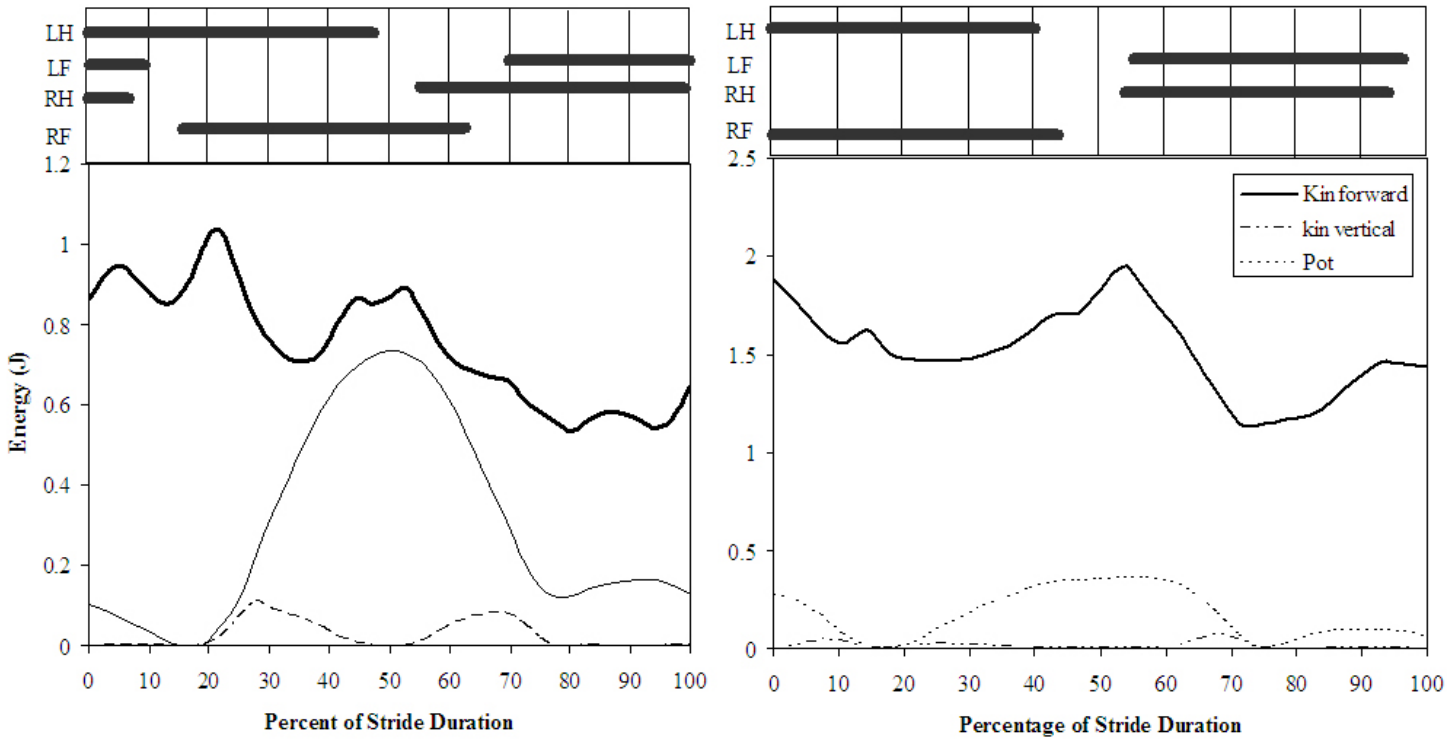


Figure 5.40. Energy changes of the center of mass during an amble (a) and a trot (b).

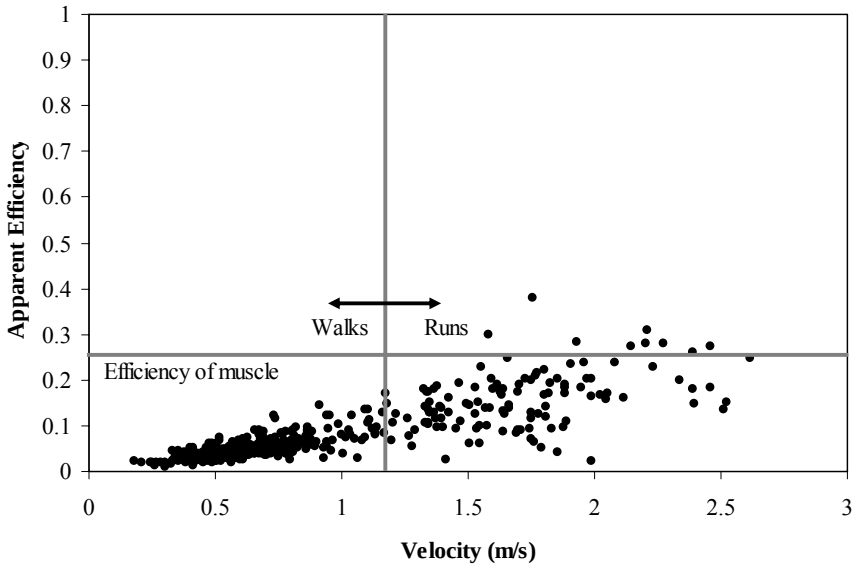


Figure 5.41. Apparent efficiency of positive work in the infant baboon sample.

Apparent efficiency is calculated as the ratio of total mechanical power output and total metabolic energy input. Apparent efficiencies above .25 indicate the probable use of elastic energy storage and recovery mechanisms.

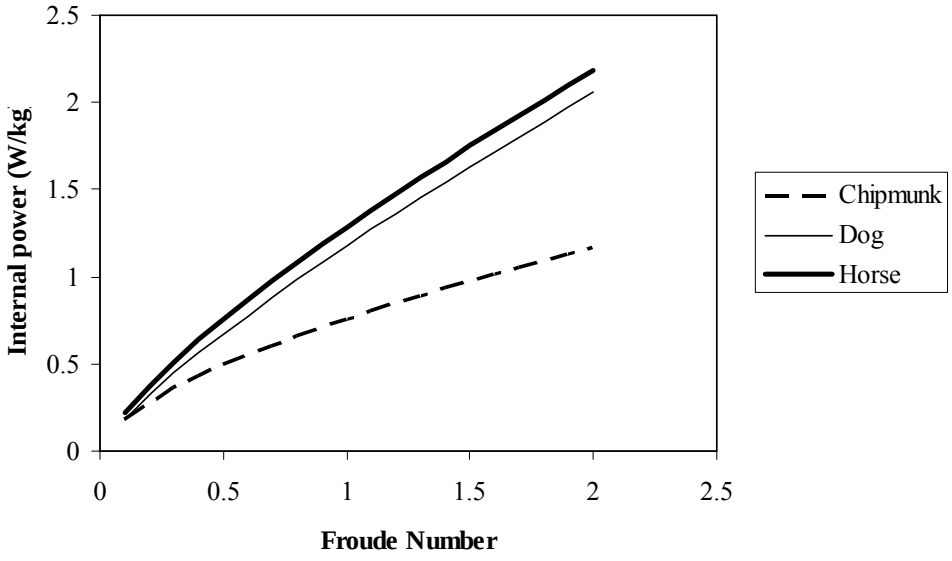


Figure 5.42. Internal power in quadrupedal mammals from Fedak et al. (1982) recalculated using the same Froude numbers.

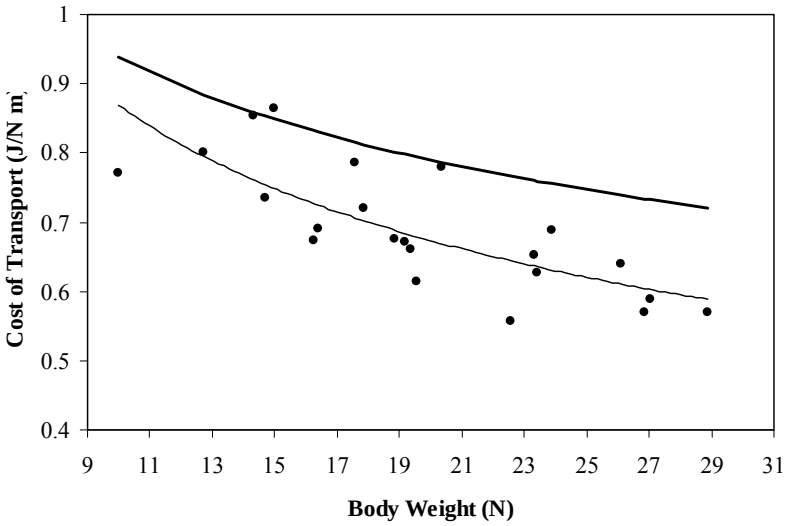


Figure 5.43. Cost of transport in the infant baboon sample compared to non-primate quadrupeds.

Cost of transport for the infant baboons are the closed circles and their trend line is represented by the thin line. The thick line is the costs of transport for non-primates from Roberts et al. (1998).

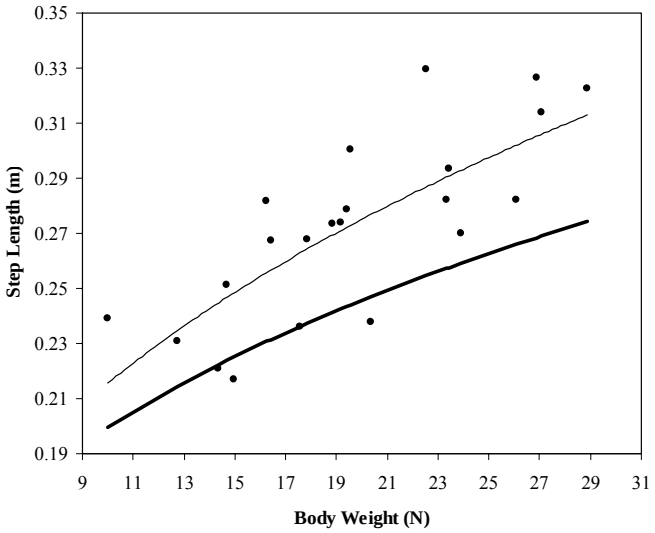


Figure 5.44. Mean step lengths for the infant baboons and non-primate quadrupeds.

Mean step lengths calculated for each sampled age in the infant baboons represented by closed circles and the thin black line. Step lengths for non-primates are the thick black line and were taken from Roberts et al. (1998).

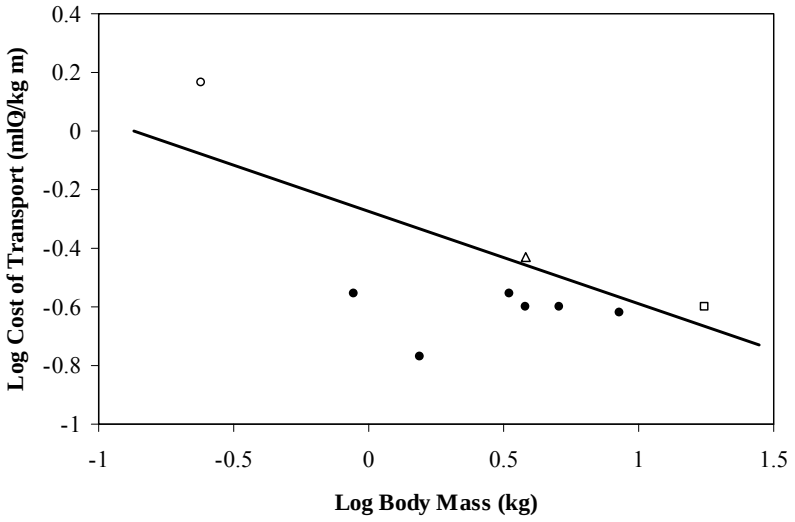


Figure 5.45. Cost of transport in primate quadrupeds compared to non-primates from Taylor et al. (1982)

Costs of transport are reported here as the slope of the regression line relating mass-specific rate of oxygen consumption with velocity. Primate quadrupeds are the closed circles, the open circle is a bush baby, the open triangle is a spider monkey, and the open square is a chimpanzee form Taylor et al. (1982). The solid black line is the all taxon least-squares regression line from Taylor et al. (1982).

CHAPTER 6

Conclusions and Future Directions

SUMMARY OF RESULTS FROM THE INFANT BABOON SAMPLE

The infant baboons sampled here undergo a transition in their limb mass distribution patterns. Their limb mass is distributed most distally at young ages, when their grasping abilities are strongest. As they age, and they become less reliant on constant grasping of their mothers' hair, their limb mass distribution pattern becomes more proximally concentrated.

In infant baboons, transitions in limb mass distribution are accompanied by transitions in kinematics. As limb mass becomes more proximally concentrated, the infant baboons use relatively higher stride frequencies and relatively shorter strides. Changes in stride length and stride frequency are brought about by changes in other spatio-temporal kinematics.

The changes in kinematics appear to offset changes in limb mass distribution so that mechanical work and power requirements do not change with age. The infant baboons do not appear to follow the mechanical work trade-off hypothesis longitudinally. This result may be caused by the rather slight changes in kinematics with age. However, when compared to other quadrupedal mammals, the infant baboons do appear to follow a mechanical power tradeoff hypothesis.

OVERALL IMPLICATIONS FOR PRIMATE EVOLUTION

The results from this study provide a morphologically based scenario for the evolution of primate quadrupedal kinematics. Given the assumption that early primate evolution was associated with a small branch environment, the earliest primates would

have evolved clawless grasping hands and feet to maneuver and manipulate food in this environment (Cartmill, 1972, 1974). The evolution of grasping hands and feet would have necessitated the evolution of heavy distal limb elements in the earliest primates. These heavy distal limb elements would have led earliest primates to walk with many of the same kinematic characteristics observed in extant primate taxa (long strides, low stride frequencies, long stance durations, and large limb angular excursions). Most importantly, the evolution of grasping hands and feet would not have come at an energetic price. Because of the possible use of a mechanical work and power tradeoff mechanism (i.e. lower internal work and power in conjunction with higher external work and power), early primates may have done similar amounts of total work and power compared to other quadrupeds of similar size. Despite the fact that the longitudinal analysis of the infant baboons did not show evidence of a trade-off mechanism, the comparative evidence strongly suggests that this mechanism is apparent when differences in kinematics are large (as would have likely been the case during early primate evolution).

The results of this study are not incompatible with the ecological hypothesis for the evolution of primate kinematics recently suggested by several researchers (Demes et al., 1990; Larson, 1998; Larson et al., 2000, 2001; Schmitt and Lemelin, 2002; Cartmill et al., 2002; Schmitt, 2003). The results from this study provide a powerful morphological explanation for the small branch niche hypothesis. The fact that primate kinematic specializations are helpful in this niche would have further reinforced their use by the earliest primates. Most importantly, the results of this study provide an explanation for why primate quadrupeds continue to use this unique suite of kinematics when they are not in a small branch niche. Additionally the results from this study explain why primates who no longer make use of this niche (e.g. dedicated terrestrial

quadrupeds and taxa that are too large to perform above-branch quadrupedalism), but who maintain grasping extremities for climbing and other manipulative needs, may still use the unique aspects of primate quadrupedalism.

OVERALL IMPLICATIONS FOR MAMMALIAN QUADRUPEDALISM

Mammalian quadrupedalism should be governed by the same principles as those described for primates. Mammals should lie on a continuum of spatio-temporal kinematics that matches a continuum in mammalian limb mass distribution patterns. Additionally, the mechanical energy tradeoff mechanism may be functioning in mammalian quadrupeds. The data sets used in Fedak et al. (1982) and Heglund et al. (1982) to conclude that internal and external work are independent of body size are extremely small. Also, velocity was not normalized in those studies to account for differences in body mass. It seems likely that empirical data over a wide range of body sizes and shapes, and the normalization of velocity, would show a broad pattern of mechanical work and power tradeoff allowing total work and power to be truly body size independent. If the tradeoff mechanism is a broad feature of mammalian locomotion, then the results of Taylor et al. (1974) are easily explained. A cheetah, a gazelle, and a goat would have similar costs of locomotion at a given velocity because they do similar amounts of total work and power at a given velocity.

FUTURE DIRECTIONS

Replication of the results from this study on a wider range of taxa is necessary to fully support the broad suggestions made above. A comparative analysis of primate taxa that differ in their limb mass distributions should be carried out. Additionally, this is the first study to calculate mechanical internal and total work, and only the second to calculate external work, in primates. There is a true lack of information regarding the

work done during primate locomotion and it is necessary to have a more complete picture of the mechanics of primate locomotion.

The limb inertial properties of non-primates who converge on primate locomotor kinematics should be calculated to examine the possibility that their kinematics are similar to primates because of the link between morphology and locomotion described in this study. A study such as this is currently being started with Pierre Lemelin on the woolly opossum.

A broader comparative analysis of mammalian quadrupeds is needed as well. Most comparative studies of mammalian quadrupedalism span an extremely large range of body sizes, yet include very few taxa (e.g. comparing a chipmunk, a dog, and a horse). Comparative mammalian studies that include taxa that are more similar in body mass, but that differ in their limb mass distribution patterns are necessary to explore the validity of generalizing the results from this study to mammalian quadrupedal evolution.

In addition to answering questions of kinematics, more research must be done to understand the determinants of the costs of locomotion in mammals. The results from this study suggest a tradeoff mechanism which renders total mechanical work and power independent of body size. So, differences in mechanical work and power outputs should not explain the differences in energetic costs related to body size described by Taylor et al. (1982). Yet, Kram and Taylor's (1990) explanation for energetic costs seems unlikely to be the true answer given the recent results of Marsh et al. (2004) showing the costs of swinging the limbs to be 25% of the total cost of locomotion at a given velocity.

OVERALL CONCLUSIONS

This study provides an example of using a combination of techniques to examine specific hypotheses. Hypotheses may be more fully tested by combining modeling

techniques, data from experimental alterations in body shapes, comparative data, and ontogenetic data.

This study provides some answers for why quadrupeds may walk and run with different kinematics, as well as why mammals that differ in body shape may not differ in their energetic costs. At present, though, we are left with a great mystery regarding the determinants of the energetic costs of locomotion. Certainly energetics has been a major selective force in the evolution of mammals so the answer to this question may be one of the most important unresolved issues in mammalian biomechanics.

One of the main problems in answering this question is that we must approach mammalian energetics from multiple directions, none of which actually measure how muscles are using energy during locomotion (although Marsh et al., 2004 have gotten very close). Heglund (2004) stated it best when describing the results of Marsh et al. (2004):

> I came across a colleague searching the grass in a circle of light under a street lamp. "What are you looking for?" I asked. "Keys," he answered, at which point I started to help him in his search. But after a while it became apparent that we were not finding any keys, so I asked, "Are you sure they're here?" to which he replied "Oh, no, they're not here, they're out there someplace," gesturing off into the darkness, "but the light's better here!"

The study of quadrupedal energetics has always focused on the variables that are measurable in live animals such as work and kinematics. At the present time, it is difficult to shine the light anywhere else. Techniques such as more intensive modeling of individual muscle energy use during locomotion (e.g. Bahrgava et al., 2004) are surely best suited to understanding the underlying determinants of the energetic costs of locomotion. This study provided an example of how relatively simple relationships

between morphology and locomotion may have great explanatory powers. Models that make use of these empirically supported relationships, combined with more detailed models of muscular energy expenditures, seems to be the most promising means of discovering the factors that contribute to the energy costs of locomotion in mammals.

APPENDIX: CALCULATION OF SEGMENT INERTIAL PROPERTIES

As noted in the text, a and b describe the lengths of the major and minor axes of the elliptical column segment model and are given by second order polynomials of the form:

$$a = ez^2 + dz + c \tag{A1}$$

$$b = kz^2 + gz + f \tag{A2}$$

The mass can then be calculated by solving the definite integral:

$$Mass = \rho \int_0^l \pi abdz \tag{A3}$$

Where πab is the area of an ellipse, ρ is the density of the segment, and l is the length of the segment. Substituting equations A1 and A2 into equation A3 and solving the definite integral gives the following equation for segment mass:

$$Mass = \rho\pi(cfz + \frac{1}{2}(df + cg)z^2 + \frac{1}{5}ekz^5 + \frac{1}{3}(ef + dg + ck)z^3 + \frac{1}{4}(eg + dk)z^4) \tag{A4}$$

The center of mass can be found by solving the definite integral:

$$CM = \frac{\int_0^l \pi abzdz}{\int_0^l \pi abdz} \tag{A5}$$

Where the denominator in equation A5 is the total mass of the segment. Substituting equations A1 and A2 into equation A5 and solving the definite integral gives the following equation for segment CM:

$$CM = \frac{(\frac{1}{2}cfz^2 + \frac{1}{3}(df + cg)z^3 + \frac{1}{6}ekz^6 + \frac{1}{4}(ef + dg + ck)z^4 + \frac{1}{5}(eg + dk)z^5}{(\frac{1}{5}ekz^5 + cfz + \frac{1}{2}(df + cg)z^2 + \frac{1}{3}(ef + dg + ck)z^3 + \frac{1}{4}(eg + dk)z^4)} \quad \text{(A6)}$$

Equation A6 gives the position of the center of mass from the distal end. Subtracting this value from the segment length will give the position of the CM. from the proximal end. Finding the moment of inertia of the segment requires the use of a double integral of the form:

$$I = 2\rho \int_0^l \int_{-a}^{a} (x^2 + z^2) dA dz \quad \text{(A7)}$$

Where dA is an area element of the form:

$$dA = 2y * dx \quad \text{(A8)}$$

Where y is from the equation for an ellipse:

$$1 = \frac{x^2}{a^2} + \frac{y^2}{b^2} \quad \text{(A9)}$$

Manipulating equation (A9) to solve for y gives:

$$y^2 = (1 - \frac{x^2}{a^2})b^2 \quad \text{(A10)}$$

Taking the square root of both sides of equation A10 gives:

$$y = b\sqrt{1 - \frac{x^2}{a^2}} \quad \text{(A11)}$$

Substituting equation A11 into equation A8 gives the equation for dA:

$$dA = 2b\sqrt{1-\frac{x^2}{a^2}}dx \tag{A12}$$

Substituting equation A12 into equation A7 gives the equation for the mass moment of inertia.

$$I = 2\rho\int_0^l\int_{-a}^{a}(x^2+z^2)b\sqrt{1-\frac{x^2}{a^2}}dxdz \tag{A13}$$

Expanding equation A13 gives:

$$I = 2\rho\int_0^l\int_{-a}^{a}(\frac{b}{a}x^2\sqrt{a^2-x^2}+\frac{b}{a}z^2\sqrt{a^2-x^2})dxdz \tag{A14}$$

Integration of equation A14 while holding z constant gives:

$$I = 2\rho\int_0^l(\frac{ba^3}{8}\pi+\frac{ba}{2}\pi z^2)dz \tag{A15}$$

Finally, substituting equations A1 and A2 into equation A15 and solving the definite integral gives the following:

$$I = 2\rho(\frac{1}{2}\pi(\frac{1}{3}cfz^3+\frac{1}{4}(df+cg)z^4+\frac{1}{7}ekz^7+\frac{1}{5}(ef+dg+ck)z^5+$$
$$\frac{1}{6}(eg+dk)z^6)+(\frac{1}{8}\pi(c^3fz+\frac{1}{2}c^2(3df+cg)z^2+\frac{1}{9}e^3kz^9+$$
$$\frac{1}{3}cz^3(3d^2f+3cef+3cdg+c^2k)+\frac{1}{8}e^2z^8(eg+3dk)+$$
$$\frac{1}{4}z^4(d^3f+6cdef+3cd^2g+3egc^2+3dkc^2)+$$
$$\frac{1}{7}ez^7(e^2f+3\deg+3d^2k+3cek)+\frac{1}{6}z^6(3de^2f+3d^2eg+3cge^2+d^3k+6cdek)+$$
$$\frac{1}{5}z^5(3d^2ef+3cfe^2+d^3g+6c\deg+3cd^2k+3c^2ek)))$$

(A16)

Equation A16 gives the moment of inertia about the distal end of the segment. To find the moment of inertia about the segment CM, the parallel axis theorem (equation A17) must be applied.

$$I_{CM} = I - (mass)(CM)^2 \qquad \text{(A17)}$$

REFERENCES

Abourachid A (2001) Kinematic parameters of terrestrial locomotion in cursorial (ratites), swimming (ducks), and striding birds (quail and guinea fowl). Comparative Biochemistry and Physiology Part A *131:*113-119.

Aerts P, Van Damme R, Van Elsacker L, and Duchene V (2000) Spatio-temporal gait characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in bonobos (*Pan paniscus*). Am. J. Phys. Anthropol. *111:*508-517.

Alexander RM (1976) Mechanics of bipedal locomotion. In PS Davies (ed.): Perspectives in Experimental Biology. Oxford: Pergamon, pp. 492-504.

Alexander RM (2003) Modelling approaches in biomechanics. Philos. Trans. R. Soc. Lond. B. Biol. Sci. *358:*1429-1435.

Alexander RM, and Jayes AS (1983) A dynamic similarity hypothesis for the gaits of quadrupedal mammals. Journal of Zoology London *201:*135-152.

Alexander RM, Jayes AS, Maloiy GMO, and Wathuta EM (1981) Allometry of the leg muscles of mammals. J. Zool. *194:*539-552.

Alexander RM, and Maloiy GMO (1984) Stride lengths and stride frequencies of primates. Journal of Zoology London *202:*577-582.

Altmann J (1980) Baboon mothers and infants. Cambridge, MA: Harvard University Press.

Anderson FC, and Pandy MG (2001) Dynamic optimization of human walking. J. Biomech. Eng. *123:*381-390.

Bhargava LJ, Pandy MG, and Anderson FC (2004) A phenomenological model for estimating metabolic energy consumption in muscle contraction. J. Biomech. *37:*81-88.

Basmajian JV (1978) Muscles alive, their functions revealed by electromyography. Baltimore: Williams and Wilkins.

Biewener AA (2003) Animal Locomotion. New York: Oxford University Press.

Biewener AA, Alexander RM, and Heglund NC (1981) Elastic energy storage in the hopping kangaroo rats (Dipodymys spectabilis). J. Zool. *195:*369-383.

Blaszczyk JW, and Dobrzecka C (1989) Speed control in quadrupedal locomotion:

Principles of limb coordination in the dog. Acta Neurobiol. Exp. (Warsz). *49:*105-124.

Carrier DR (1996) Ontogenetic limits on locomotor performance. Physiol. Zool. *69:*467-488.

Cartmill M (1972) Arboreal adaptations and the origin of the order primates. In RH Tuttle (ed.): The Functional and Evolutionary Biology of Primates. Chicago: Aldine-Atherton, pp. 3-35.

Cartmill M (1974) Rethinking primate origins. Science *184:*436-443.

Cartmill M (1992) New views on primate origins. Evolutionary Anthropology *1:*105-111.

Cartmill M, Lemelin P, and Schmitt D (2002) Support polygons and symmetrical gaits in mammals. Zoological Journal of the Linnean Society *136:*401-420.

Cavagna GA, and Franzetti P (1986) The determinants of the step frequency in walking in humans. J. Physiol. (Lond). *373:*235-242.

Cavagna GA, Heglund NC, and Taylor CR (1977) Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. Am. J. Physiol. *233:*R243-R261.

Cavagna GA, and Kaneko M (1977) Mechanical work and efficiency in level walking and running. J. Physiol. (Lond). *268:*467-481.

Cavagna GA, Willems PA, Franzetti P, and Detrembleur C (1991) The two power limits conditioning step frequency in human running. J. Physiol. (Lond). *437:*95-108.

Crompton RH, Li Y, Alexander RM, Wang W, and Gunther MM (1996) Segment inertial properties of primates: New techniques for laboratory and field studies of locomotion. Am. J. Phys. Anthropol. *99:*547-570.

Crompton RH, Li Y, Wang WJ, Gunther M, and Savage R (1998) The mechanical effectiveness of erect and "bent-hip, bent-knee" bipedal walking in *Australopithecus afarensis*. J. Hum. Evol. *35:*55-74.

Dagg AI (1973) Gaits in mammals. Mammalian Review *3:*135-154.

DeJaeger D, Willems PA, and Heglund NC (2001) The energy cost of walking in children. Pflugers Archive - European Journal of Physiology *441:*538-543.

Dellanini L, Hawkins D, Martin RB, and Stover S (2003) An investigation of the

interactions between lower-limb bone morphology, limb inertial properties and limb dynamics. J. Biomech. *36:*913-919.

Demes B, Jungers WL, and Nieschalk U (1990) Size- and speed related aspects of quadrupedal walking in slender and slow lorises. In FK Jouffroy, MH Stack and C Niemitz (eds.): Gravity, Posture and Locomotion in Primates. Firenze: Il Sedicesimo, pp. 175-197.

Demes B, Larson SG, Stern JT, Jungers WL, Biknevicius AR, and Schmitt D (1994) The kinetics of primate quadrupedalism: "Hindlimb drive" reconsidered. J. Hum. Evol. *26:*353-374.

Demes B, Stern JT, Hausman MR, Larson SG, Mcleod KJ, and Rubin CT (1998) Patterns of strain in the macaque ulna during functional activity. Am. J. Phys. Anthropol. *106:*87-100.

Dunbar DC, and Badam GL (1998) Development of posture and locomotion in free-ranging primates. Neurosci. Biobehav. Rev. *22:*541-546.

English AW (1978) Functional analysis of the shoulder girdle of cats during locomotion. J. Morphol. *156:*279-292.

Fancy SG, and White RG (1987) Energy expenditures for locomotion by barren-ground caribou. Can. J. Zool. *65:*122-128.

Farley CT, Glasheen J, and McMahon TA (1993) Running springs: Speed and animal size. J. Exp. Biol. *185:*71-86.

Fedak MA, Heglund NC, and Taylor CR (1982) Energetics and mechanics of terrestrial locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals. J. Exp. Biol. *79:*23-40.

Fenn WO (1930) Work against gravity and work due to velocity changes in running. Am. J. Physiol. *93:*433-462.

Fleagle JG (1998) Primate Adaptation and Evolution. New York: Academic Press, Inc.

Gebo D (1997) Locomotor diversity in prosimian primates. Am. J. Primatol. *13:*271-281.

Goslow GEJ, Seeherman HJ, Taylor CR, McCutchin MN, and Heglund NC (1981) Electrical activity and relative length changes of dog limb muscles as a function of speed and gait. J. Exp. Biol. *94:*15-42.

Grand TI (1977a) Body weight: Its relation to tissue composition, segment distribution,

and motor function. I. Interspecific comparisons. Am. J. Phys. Anthropol. *47:*211-240.

Grand TI (1977b) Body weight: Its relation to tissue composition, segment distribution, and motor function. II. Development of Macaca mulatta. Am. J. Phys. Anthropol. *47:*241-248.

Grand TI (1983) Body weight: Its relationship to tissue composition, segmental distribution of mass, and motor function. 3. The didelphidae of French-Guyana. Aust. J. Zool. *31:*299-312.

Griffin TM, Roberts TJ, and Kram R (2003) Metabolic cost of generating muscular force in human walking: Insights from load-carrying and speed experiments. J. Appl. Physiol. *95:*172-183.

Hamrick MW (1998) Functional and adaptive significance of primate pads and claws: Evidence from New World anthropoids. Am. J. Phys. Anthropol. *106:*113-127.

Heglund NC (1985) Comparative energetics and mechanics of locomotion: How do primates fit in? In WL Jungers (ed.): Size and Scaling in Primate Biology. New York: Plenum Press, pp. 319-335.

Heglund NC (2004) Running a-fowl of the law. Science *303:*47-48.

Heglund NC, Cavagna GA, and Taylor CR (1982) Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. J. Exp. Biol. *79:*41-56.

Heglund NC, Fedak MA, Taylor CR, and Cavagna GA (1982) Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. J. Exp. Biol. *97:*57-66.

Heglund NC, and Schepens B (2003) Ontogeny recapitulates phylogeny? Locomotion in children and other primitive hominids. In VL Bels, JP Gasc and A Casinos (eds.): Vertebrate Biomechanics and Evolution. Oxford: BIOS Scientific Publishers Ltd, pp. 283-295.

Heglund NC, and Taylor CR (1988) Speed, stride frequency and energy cost per stride: How do they change with body size and gait? J. Exp. Biol. *138:*301-318.

Heglund NC, Taylor CR, and McMahon TA (1974) Scaling stride frequency and gait to animal sizes: Mice to horses. Science *186:*1112-1113.

Hildebrand M (1966) Analysis of the symmetrical gaits of tetrapods. Folia Biotheoretica

*6:*9-22.

Hildebrand M (1967) Symmetrical gaits of primates. Am. J. Phys. Anthropol. *26:*119-130.

Hildebrand M (1980) The adaptive significance of tetrapod gait selection. American Zoology *20:*255-267.

Hildebrand M (1985) Walking and running. In M Hildebrand, DM Bramble, KF Liem and DB Wake (eds.): Functional vertebrate morphology. Cambridge: Harvard University Press, pp. 38-57.

Hildebrand M, and Hurley J (1985) Energy of the oscillating legs of a fast-moving cheetah, pronghorn, jackrabbit, and elephant. J. Morphol. *184:*23-31.

Hof AL (1996) Scaling gait data to body size. Gait Posture *4:*222-223.

Holt KG, Hamill J, and Andres RO (1991) Predicting the minimal energy costs of human walking. Med. Sci. Sports Exerc. *23:*491-498.

Holt KG, Hammil J, and Andres RO (1990) The force-driven harmonic oscillator as a model for human locomotion. Human Movement Science *9:*55-68.

Hoyt DF, and Taylor CR (1981) Gait and the energetics of locomotion in horses. Nature *292:*239-240.

Hoyt DF, Wickler SJ, and Cogger EA (2000) Time of contact and step length: The effect of limb length, running speed, load carrying and incline. J. Exp. Biol. *203:*221-227.

Hutchinson JR, Famini D, Lair R, and Kram R (2003) Are fast-moving elephants really running? Nature *422:*493-494.

Inman VT, Ralston HJ, and Todd B (1981) Human Walking. Baltimore: Williams and Wilkins.

Irschick DJ, and Jayne BC (2000) Size matters: Ontogenetic variation in the three-dimensional kinematics of steady-speed locomotion in the lizard Dipsosaurus dorsalis. J. Exp. Biol. *203:*2133-2148.

Janis CM, and Wilhelm PB (1993) Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. Journal of Mammalian Evolution *1:*103-125.

Jenkins FAJ (1971) Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. J. Zool. *165:*303-315.

Jones FW (1916) Arboreal Man. London: Arnold.

Jungers WL, and Stern JT (1983) Body proportions, skeletal allometry and locomotion in Hadar hominids: A reply to Wolpoff. J. Hum. Evol. *12:*673-684.

Kimura T, Okada M, and Ishida H (1979) Kinesiological characteristics of primate walking: its significance in human walking. In ME Morbek, H Preuschoft and N Gomberg (eds.): Environment, Behavior, and Morphology: Dynamic Interactions in Primates. New York: G. Fischer, pp. 297-311.

Kram R, and Taylor CR (1990) Energetics of running: A new perspective. Nature *346:*265-267.

Kramer PA (1999) Modelling the locomotor energetics of extinct hominids. J. Exp. Biol. *202:*2807-2818.

Lammers AR, and German RZ (2002) Ontogenetic allometry in the locomotor skeleton of specialized half-bounding mammals. J. Zool. *258:*485-495.

Larney E, and Larson SG (in press) Compliant walking in primates: Elbow and knee yield in primates compared to other mammals. Am. J. Phys. Anthropol.

Larson SG (1993) Functional morphology of the shoulder in primates. In DL Gebo (ed.): Postcranial Adaptations in Nonhuman Primates. DeKalb: Norther Illinois University Press, pp. 45-69.

Larson SG (1998) Unique aspects of quadrupedal locomotion in nonhuman primates. In E Strasser, J Fleagle, A Rosenberger and H McHenry (eds.): Primate locomotion: Recent advances. New York: Plenum Press, pp. 157-174.

Larson SG, Schmitt D, Lemelin P, and Hamrick M (2000) Uniqueness of primate forelimb posture during quadrupedal locomotion. America Journal of Physical Anthropology *112:*87-101.

Larson SG, Schmitt D, Lemelin P, and Hamrick M (2001) Limb excursion during quadrupedal walking: how do primates compare to other mammals? Journal of Zoology, London *255:*353-365.

Larson SG, and Stern JT (1989) The role of propulsive muscles of the shoulder during quadrupedalism in vervet monkeys (Cercopithecus aethiops): Implications for neural control of locomotion in primates. Journal of Motor Behavior *21:*457-472.

Larson SG, and Stern JT (2004) Muscle recruitment in primates: Preliminary results on

the question of neuromuscular conservation in primates. Am. J. Phys. Anthropol. *Suppl. 38:*132.

Le Gros Clark WE (1934) Early Forerunners of Man. Baltimore: William Wood.

Le Gros Clark WE (1959) The Antecedents of Man. Edinburgh: Edinburgh University Press.

Lemelin P (1996) The evolution of manual prehensility in primates: A comparative study of prosimians and didelphid marsupials, State University of New York at Stony Brook.

Lemelin P (1999) Morphological correlates of substrate use in didelphid marsupials: Implications for primate origins. J. Zool. *247:*165-175.

Leonard WR, and Robertson ML (1997) Comparative primate energetics and hominid evolution. Am. J. Phys. Anthropol. *102:*265-281.

Leonard WR, and Robertson ML (1997) Rethinking the energetics of bipedality. Current Anthropology *38:*304-309.

Leonard WR, and Robertson ML (2001) Locomotor economy and the origin of bipedality: Reply to Steudel-Numbers. Am. J. Phys. Anthropol. *116:*174-176.

Marsh RL, Ellerby DJ, Carr JA, Havalee TH, and Buchanan CI (2004) Partitioning the energetics of walking and running: Swinging the limbs is expensive. Science *303:*80-83.

Martin PE (1985) Mechanical and physiological responses to lower extremity loading during running. Med. Sci. Sports Exerc. *17:*427-433.

Mattes SJ, Martin PE, and Royer TD (2000) Walking symmetry and energy cost in persons with unilateral transtibial amputations: Matching prosthetic and intact inertial properties. Arch. Phys. Med. Rehabil. *81:*561-568.

McGreer T (1990a) Passive bipedal running. Proc. R. Soc. Lond. B. Biol. Sci. *240:*107-134.

McGreer T (1990b) Passive dynamic walking. International Journal of Robotics Research *9:*62-82.

McHenry HM (1991) First steps? Analyses of the postcranium of early hominids. In Y Coppens and B Senut (eds.): Origine(s) de la Bipedie chez les Hominides (Cahiers de Paleoanthropologie). Paris: Editions du CNRS, pp. 133-141.

McMahon TA (1975) Using body size to understand the structural design of animals: Quadrupedal locomotion. J. Appl. Physiol. *39:*619-627.

Minetti AE (1998) The biomechanics of skipping gaits: a third locomotor paradigm? Proc. R. Soc. Lond. B. Biol. Sci. *265:*1227-1235.

Minetti AE, Ardigo LP, Reinach E, and Saibene F (1999) The relationship between mechanical work and energy expenditure of locomotion in horses. J. Exp. Biol. *202:*2329-2338.

Minetti AE, Capelli C, Zamparo P, Prampero PE, and Saibene F (1995) Effects of stride frequency on mechanical power and energy expenditure of walking. Med. Sci. Sports Exerc. *27:*1194-1202.

Minetti AE, and Saibene F (1992) Mechanical work rate minimization and freely chosen stride frequency of human walking: A mathematical model. J. Exp. Biol. *170:*19-34.

Mochon S, and McMahon TA (1980) Ballistic walking. J. Biomech. *13:*49-57.

Mochon S, and McMahon TA (1981) Ballistic walking: An improved model. Math. Biosci. *52:*241-260.

Muybridge E (1887) Animals in Motion. London: Chapman and Hall.

Myers G, and Steudal K (1985) Effect of limb mass and its distribution on the energetic cost of running. J. Exp. Biol. *116:*363-373.

Myers MJ, and Steudel K (1997) Morphological conservation of limb Natural Pendular Period in the domestic dog (*Canis familiaris*): Implications for locomotor energetics. J. Morphol. *234:*183-196.

Napier JR (1993) Hands. Princeton, N.J.: Princeton University Press.

Parchman AJ, Reilly SM, and Biknevicius A (2003) Whole-body mechanics and gaits in the gray short-tailed opossum Monodelphis domesticus: integrating patterns of locomotion in a semi-erect mammal. J. Exp. Biol. *206:*1379-1388.

Pasi BM, and Carrier DR (2003) Functional trade-offs in the limb muscles of dogs selected for running vs. fighting. Journal of Evolutionary Biology *16:*324-332.

Pilbeam D (1986) Distinguished lecture: Hominoid evolution and hominoid origins. American Anthropol. *88:*295-312.

Polk J (2001) The influence of body size and body proportions on primate quadrupedal

locomotion. Dissertation, State University of New York at Stony Brook, Stony Brook.

Polk JD (2002) Adaptive and phylogenetic influences on musculoskeletal design in cercopithecine primates. J. Exp. Biol. *205:*3399-3412.

Preuschoft H, and Gunther MM (1994) Biomechanics and body shape in primates compared with horses. Zietschrift fur Morphologie und Anthropologie *80:*149-165.

Raichlen DA (2004) Convergence of forelimb and hindlimb natural pendular periods in baboons (*Papio cynocephalus*) and its implication for the evolution of primate quadrupedalism. J. Hum. Evol.*46:*719-738.

Rasmussen DT (1990) Primate origins: Lessons from a neotropical marsupial. Am. J. Primatol. *22:*263-277.

Reilly SM (2000) Locomotion in the quail (Corturnix japonica): The kinematics of walking and increasing speed. J. Morphol. *243:*173-185.

Reilly SM, and Biknevicius A (2003) Integrating kinetic and kinematic approaches to the analysis of terrestrial locomotion. In VL Bels, JP Gasc and A Casinos (eds.): Vertebrate Biomechanics and Evolution. Oxford: BIOS Scientific Publishers Ltd, pp. 243-265.

Reynolds HM (1974) Measurement of the inertial properties of the segmented savannah baboon. PhD dissertation, Southern Methodist University.

Reynolds TR (1985) Stresses on the limbs of quadrupedal primates. Am. J. Phys. Anthropol. *67:*101-116.

Reynolds TR (1987) Stride length and its determinants in humans, early hominids, primates, and mammals. Am. J. Phys. Anthropol. *72:*101-115.

Roberts TJ, Kram R, Weyand PG, and Taylor CR (1998) Energetics of bipedal running I. Metabolic cost of generating force. J. Exp. Biol. *201:*2745-2751.

Roberts TJ, Marsh RL, Weyand PG, and Taylor CR (1997) Muscular force in running turkeys: The economy of minimizing work. Science *275:*1113-1115.

Rodman PS, and McHenry HM (1980) Bioenergetics and the origin of hominid bipedalism. Am. J. Phys. Anthropol. *52:*103-106.

Rollinson J, and Martin RD (1981) Comparative aspects of primate locomotion, with

special reference to arboreal cercopithecines. Symp. Zool. Soc. Lond. *48:*377-427.

Schepens B, Bastien GJ, Heglund NC, and Willems PA (2004) Mechanical work and muscular efficiency in walking children. J. Exp. Biol. *207:*587-596.

Schepens B, Willems PA, Cavagna GA, and Heglund NC (2001) Mechanical power and efficiency in running children. Pflugers Archive *442:*107-116.

Schmidt-Nielsen K (1984) Scaling: Why is animal size so important? Cambridge: Cambridge University Press.

Schmitt D (1994) Forelimb mechanics as a function of substrate type during quadrupedalism in 2 anthropoid primates. J. Hum. Evol. *26:*441-457.

Schmitt D (1998) Forelimb mechanics during arboreal and terrestrial quadrupedalism in Old World monkeys. In E Strasser, J Fleagle, A Rosenberger and H McHenry (eds.): Primate Locomotion: Recent Advances. New York: Plenum Press, pp. 175-200.

Schmitt D (1999) Compliant walking in primates. J. Zool. *247:*149-160.

Schmitt D (2003) Evolutionary implications of the unusual walking mechanics of the common marmoset (*Callithrix jacchus*). Am. J. Phys. Anthropol. *122:*28-37.

Schmitt D (2003) Substrate size and primate forelimb mechanics: Implications for understanding the evolution of primate locomotion. International Journal of Primatology *24:*1023-1036.

Schmitt D, Larson SG, and Stern JT (1994) Serratus ventralis function in vervet monkeys (*Cercopithecus aethiops*): are primate quadrupeds unique? Journal of Zoology, London *232:*215-230.

Schmitt D, and Lemelin P (2002) The origins of primate locomotion: gait mechanics of the woolly opossum. Am. J. Phys. Anthropol. *118:*231-238.

Schmitt D, Lemelin P, and Hanna JB (2003) Locomotor modes of primates at moderate speeds. I. The implications of the amble and the canter for primate locomotor evolution. Am. J. Phys. Anthropol. *Suppl. 36:*185.

Selles RW, Bussmann BJ, Wagenaar RC, and Stam HJ (2001) Comparing predictive validity of four ballistic swing phase models of human walking. J. Biomech. *34:*1171-1177.

Shapiro LJ, and Raichlen DA (in press) Lateral sequence walking in infant *Papio*

cynocephalus: Implications for the evolution of diagonal sequence walking in primates. Am. J. Phys. Anthropol.

Skinner HB, and Barrack RL (1990) Ankle weighting effect on gait in able-bodied adults. Arch. Phys. Med. Rehabil. *71:*112-115.

Sokal RR, and Rohlf FJ (1995) Biometry. New York: Freeman.

Sprigings F, and Leach D (1986) Standardized technique for determining the center of gravity of body and limb segments of horses. Equine Vet. J. *18:*43-49.

Steudel K (1990) The work and energetic cost of locomotion. I. The effects of limb mass distribution in quadrupeds. J. Exp. Biol. *154:*273-285.

Steudel K (1990) The work and energetic cost of locomotion. II. Partitioning the cost of internal and external work within a species. Journal of Experimental Biology *154:*287-303.

Steudel K (1996) Limb morphology, bipedal gait, and the energetics of hominid locomotion. Am. J. Phys. Anthropol. *99:*345-355.

Steudel-Numbers KA (2003) The energetic cost of locomotion: humans and primates compared to generalized endotherms. J. Hum. Evol. *44:*255-262.

Strang KT, and Steudal K (1990) Explaining the scaling of transport costs: the role of stride frequency and stride length. Journal of Zoology, London *221:*343-358.

Sussman RW (1991) Primate origins and the evolution of angiosperms. Am. J. Primatol. *23:*209-223.

Taylor CR (1985) Force development during sustained locomotion: A determinant of gait, speed and metabolic power. J. Exp. Biol. *115:*253-262.

Taylor CR (1994) Relating mechanics and energetic during exercise. Adv. Vet. Sci. Comp. Med. *38:*181-215.

Taylor CR, Heglund NC, and Maloiy GMO (1982) Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of body size in birds and mammals. J. Exp. Biol. *97:*1-21.

Taylor CR, Heglund NC, McMahon TA, and Looney TR (1980) Energetic cost of generating muscular force during running: A comparison of large and small animals. J. Exp. Biol. *86:*9-18.

Taylor CR, Shkolnik A, Dmpel R, Baharav D, and Borut A (1974) Running in cheetahs,

gazelles, and goats: energy cost and limb configuration. Am. J. Physiol. *227:*848-850.

Tipler PA (1976) Physics. New York: Worth.

Turnquist JE, and Wells JP (1994) Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. J. Hum. Evol. *26:*487-499.

Turvey MT, Schmidt RC, and Rosenblum LD (1988) On the time allometry of co-ordinated rhythmic movements. J. Theor. Biol. *130:*285-325.

Vilensky JA (1979) Masses, centers-of-gravity, and moments-of-inertia of the body segments of the Rhesus monkey (*Macaca mulatta*). Am. J. Phys. Anthropol. *50:*57-65.

Vilensky JA (1983) Gait characteristics of two macaques, with emphasis on relationships with speed. Am. J. Phys. Anthropol. *61:*255-265.

Vilensky JA (1987) Locomotor behavior and control in human and nonhuman primates: Comparisons with cats and dogs. Neurosci. Biobehav. Rev. *11:*263-274.

Vilensky JA (1989) Primate quadrupedalism: How and why does it differ from that of typical quadrupeds. Brain Behavior and Evolution *34:*357-364.

Vilensky JA, and Gankiewicz A (1990) Effects of speed on forelimb joint angular displacement patterns in vervet monkeys (*Cercopithecus aethiops*). Am. J. Phys. Anthropol. *83:*203-210.

Vilensky JA, Gankiewicz A, and Townsend DW (1990) Effects of size on vervet (*Cercopithecus aethiops*) gait parameters - A longitudinal approach. Am. J. Phys. Anthropol. *81:*429-439.

Vilensky JA, and Gankiewicz E (1986) Effects of size on vervet (*Cercopithecus aethiops*) gait parameters - a preliminary analysis. Folia Primatol. (Basel). *46:*104-117.

Vilensky JA, Gankkiewicz E, and Townsend DW (1988) Effects of size on vervet (*Cercopithecus aethiops*) gait parameters: A cross sectional approach. Am. J. Phys. Anthropol. *76:*463-480.

Vilensky JA, and Gehlson G (1984) Temporal gait parameters in Humans and quadrupeds: How do they change with speed? Journal of Human Movement Studies *10:*175-188.

Vilensky JA, and Larson SG (1989) Primate locomotion: Utilization and control of symmetrical gaits. Annual Review of Anthropology *18:*7-35.

Vilensky JA, and Patrick MC (1985) Gait characteristics of 2 squirrel monkeys, with emphasis on relationships with speed and neural control. Am. J. Phys. Anthropol. *68:*429-444.

Wang WJ, Crompton RH, Li Y, and Gunther MM (2003) Energy transformation during erect and 'bent-hip, bent-knee' walking by humans with implications for the evolution of bipedalism. J. Hum. Evol. *44:*563-579.

Wells JP, and DeMenthon DF (1987) Measurements of the body segment mass, center of gravity, and determination of moments of inertia by double pendulum in *Lemur fulvus*. Am. J. Primatol. *12:*299-308.

Wells JP, and Turnquist JE (2001) Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): II. Postural and locomotor behavior and habitat use in a free-ranging colony. Am. J. Phys. Anthropol. *115:*80-94.

Whitehead PF, and Larson SG (1994) Shoulder motion during quadrupedal walking in *Cercopithecus aethiops*: Integration of cineradiographic and electromyographic data. J. Hum. Evol. *26:*525-544.

Whittlesey SN, van Emmerick REA, and Hammill J (2000) The swing phase of human walking is not a passive movement. Motor Control *4:*273-292.

Wickler SJ, Hoyt DF, Cogger EA, and Myers G (2003) The energetics of the trot-gallop transition. J. Exp. Biol. *206:*1557-1564.

Willems PA, Cavagna GA, and Heglund NC (1995) External, internal and total work in human locomotion. J. Exp. Biol. *198:*379-393.

Williams TM (1983) Locomotion in the North American mink, a semi-aquatic mammal. 2. The effect of an elongate body on running energetics and gait patterns. J. Exp. Biol. *105:*283-295.

Williams TM, Ben-David M, Noren S, Rutishauser M, McDonald K, and Heyward W (2002) Running energetics of the North American river otter: Do short legs necessarily reduce efficiency on land? Comparative Biochemistry and Physiology Part A *133:*203-212.

Winter DA (1990) Biomechanics and Motor Control of Human Movement. New York:

Wiley.

Woledge RC, Curtin NA, and Homsher E (1985) Energetic aspects of muscle contraction. London: Academic Press.

Zijlstra W, Prokop T, and Berger W (1996) Adaptability of leg movements during normal treadmill walking and split-belt walking in children. Gait Posture *4:*212-221.

VITA

David Allan Raichlen was born on December 8th, 1975 in Pasadena, California to Judith and Frederic Raichlen. After completing high school at Polytechnic School in Pasadena, CA in 1994, he entered Duke University. He graduated *cum laude* in 1998 with a B.S. in Biological Anthropology and Anatomy. He enrolled at the University of Texas at Austin in the fall of 1998.

Permanent address: 2157 Homet Rd.

San Marino, CA 91108

This dissertation was typed by the author.